Effects of Salinity and Temperature on Embryonic Development of the Pacific Cod (*Gadus macrocephalus*)[1]

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ABSTRACT

Eggs of the Pacific cod (*Gadus macrocephalus* Tilesius) were held from fertilization to completion of hatching in various combinations of constant salinity (19–31‰) and temperature (2–10 C). Hatching occurred in all salinities and temperatures, and survival was highest at the lower levels of both factors. A direct and approximately linear relationship was found between rate of development and temperature within the temperature range employed. At each temperature the length of the incubation period was increased at lower salinities. It is suspected that eggs were subjected to hypoxial conditions in the experiments, a circumstance considered to have depressed survival rate over all experimental combinations. There was, in general, an inverse relationship between salinity and temperature with respect to both size of larvae produced and the duration of the hatching period. Calculated response isopleths suggest that eggs of *Gadus macrocephalus* are euryhaline, and that maximum hatching success may be found in the vicinity of 19‰ S and 5 C. Changes of 1 C were calculated to be equivalent in effect on hatching success to a change of about 1.2‰ S.

INTRODUCTION

In Canadian waters Pacific cod (*Gadus macrocephalus* Tilesius) are close to the southern limit of their range in the northeast Pacific (Ketchen, 1961). As part of a program to investigate factors which may limit abundance in Canadian waters, Forrester (1964) studied effects of temperature on development and survival of eggs of this species. Earlier investigations (Yamamoto, 1939; Yamamoto and Nishioka, 1952; Mukhacheva and Zviagina, 1960) conducted on Pacific cod in western Pacific waters were also concerned with the effects of temperature on development of the cod egg. There appears to be little evidence on the quantitative effects of salinity with respect to egg development and survival and the present study was designed to determine the effects of both salinity and temperature on aspects of survival and development of the Pacific cod egg.

MATERIALS AND METHODS

Pacific cod eggs were obtained on two occasions for these studies. Live cod were captured by trawl net on February 24 and March 11, 1965, from a depth of 40–48 fath on a spawning ground at Nanoose Bay in the Strait of Georgia, British Columbia (48°15′N lat, 124°W long). The cod were transported to the Biological Station, Nanaimo, where fertilization was effected by stripping

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eggs and milt into a plastic container of sea water and gently stirring the mixture. Transfer of eggs to experimental conditions was made within 1 hr following fertilization.

Studies were conducted in a battery of identical 35-liter insulated plastic tanks. Samples of 1000–2000 eggs (sp gr = 1.049 at 20 C) were incubated in 3-inch diameter cylindrical containers of plastic and nylon-mesh construction. Four such subsamples were held in each of 13 combinations of constant salinity (‰ S) and temperature (C) and incubated until the completion of hatching, or until it was evident that no hatch would occur.

In the preparation of test waters of known salinity some salinity levels were required which were higher than that of the sea water normally available in the laboratory. Accordingly, artificial sea salt was prepared from the formula of Lyman and Fleming (Sverdrup et al., 1946) and was used in preparing the test waters. A possible bias from use of artificial sea salt was minimized by adjusting test waters from ambient salinity (27–29‰) to 37‰ with artificial sea salt, followed by dilution with fresh water to required salinity levels.

Water in each test tank was oxygenated and circulated over and through the egg containers by introducing compressed air into the tanks through porous cylindrical air stones. Test waters were exchanged every 4 days. Temperatures were checked at least three times daily throughout the course of each test.

Test conditions were set up basically according to a 3^2 factorial design, using the two experimental factors, salinity and temperature, at three levels.[2] A further set of four orthogonal contrasts was added later to the basic design. The position of each test combination in the experimental array was assigned by a random process. Mean salinity and temperature levels for the 13 incubation conditions investigated are listed in Table I.

The four subsamples of eggs in each test were positioned in a horizontal rectangular array in the centre of each tank. The egg containers were permuted through one position daily to average over the four subsamples any bias resulting from position in the tank.

Observations on development of eggs were recorded daily from the basket occupying the extreme right-hand quadrant in each test condition. Each basket remained closed until hatching commenced, or until it was considered that there would be no live hatch. Once hatching had commenced, larvae were removed from each basket not less frequently than twice in a 24-hr interval. Larval size was determined in terms of total length of larvae as measured with microscope and eyepiece micrometer disc. Those larvae showing curvature of the body were not measured; in large samples only a portion of the

[2]The original design of the experiment (February 24, 1965) was a 3^2 factorial with temperatures of 2, 6, and 10 C and salinities of 25‰, 31‰, and 37‰. No live hatch was obtained in 37‰ S at any of the temperatures. However, the structure of the design was retained by the addition of a further series of tests at 19‰ S for each temperature. In addition, one test at 6 C and 31‰ S showed abnormally high mortality of eggs with no hatching, and this particular combination was repeated in the second portion of the experiment at which time the 22‰ and 28‰ S tests were added (March 11, 1965).

TABLE I. Salinity and temperature conditions for the test combinations investigated.

Factor levels		Dates of testing (1965)	Test conditions	
			Mean ± 1 standard error	
S‰	T(C)		S‰	T(C)
19	2	11/3–14/4	19.02±0.00	2.00±0.00
19	6	11/3– 1/4	19.00±0.00	6.04±0.03
19	10	11/3–25/3	19.00±0.00	10.00±0.01
25	2	24/2– 2/4	25.05±0.02	2.02±0.01
25	6	24/2–14/3	25.01±0.00	6.01±0.01
25	10	24/2– 8/3	25.18±0.12	10.00±0.00
31	2	24/2–29/3	30.99±0.00	2.03±0.01
31	6	11/3–29/3	31.02±0.00	6.02±0.01
31	10	24/2– 8/3	31.00±0.06	10.00±0.01
22	4	11/3–13/4	21.98±0.00	4.07±0.03
22	8	11/3–27/3	22.00±0.00	8.04±0.03
28	4	11/3– 2/4	27.97±0.00	4.14±0.06
28	8	11/3–29/3	27.98±0.00	8.06±0.03

total number of larvae was measured. No attempt was made to retain larvae which were removed from the baskets.

Development time, the time in days to reach a particular developmental state, was noted according to the following easily identified stages.

I. Migration of the germ ring past equator.

II. One-half circumference of yolk surrounded by embryo.

III. Three-quarter circumference of yolk surrounded by embryo.

IV. Embryo full circle.

V. Appearance of first hatched larva. The time at which the first larva hatched was not actually observed. It was considered to be the mid point of the interval between the time of observation of the first larva hatched and that of the immediately preceding observation.

VI. Larvae 50% hatched. Hatching times in each sample were approximately normally distributed. Estimates of the time at which 50% hatch was achieved were obtained graphically from a plot of arithmetic–time probit–response distributions (Bliss, 1937).

Development time for stages I–IV was taken as the interval between fertilization and the first observation at which at least one-half of a sample of eggs had reached the stage considered. Estimates of the incubation period, the time interval between fertilization and 50% hatch, are based on the number of eggs in each sample which eventually produced viable larvae. Duration of hatching is defined as the interval between stage V and the time at which the last hatched larva was recorded. Finally, hatching efficiency is considered in terms of the initial number of eggs in each sample and the proportion of these eggs which produced live larvae.

RESULTS

Rate of Development

Development times for eggs held at the various salinities and temperatures are listed in Table II and illustrated in Fig. 1. Incubation periods ranged from approximately 8.8 days at 10 C (31‰ S) to 28.9 days at 2 C (19‰ S). Incubation periods were converted to rates of development (Krogh, 1914) and are expressed as 100 times the reciprocal of the time in days from fertilization to 50% hatching $\left(\frac{1}{T} \times 100\right)$. These rates have been plotted against temperature in Fig. 2 for comparison with results from earlier experiments (Forrester, 1964) and those of other investigators (Yamamoto, 1939; Yamamoto and Nishioka, 1952; Mukhacheva and Zviagina, 1960).

In all temperatures, time to 50% hatch appeared to be slightly increased by reduction in salinity (Fig. 3).

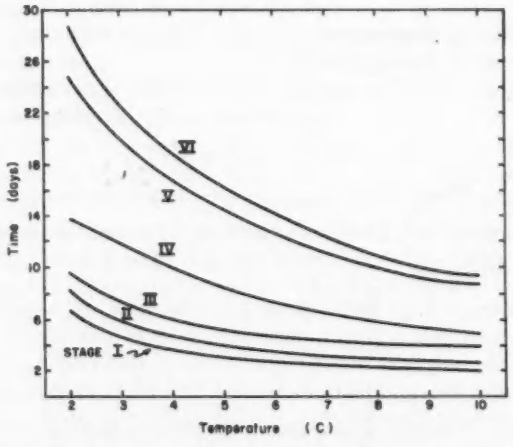

FIG. 1. Time in days to six developmental stages for eggs of Pacific cod held at constant temperatures from 2 to 10 C (see Table II and text).

TABLE II. Time in days to attain six developmental stages for Pacific cod eggs incubated at 16 salinity–temperature combinations within the range of 19–37‰ S and 2–10 C. In those cases where no entry occurs there was no live hatch.

Stage of development	Temperature (*C*)															
	2				4		6				8		10			
	Salinity (‰ S)															
	19	25	31	37	22	28	19	25	31	37	22	28	19	25	31	37
I	6.8	6.8	6.8	6.8	3.8	3.8	2.9	3.0	3.0	3.0	<3.0	<3.0	2.0	2.0	2.0	2.0
II	7.8	7.8	7.8	7.8	4.8	4.8	3.8	3.9	3.9	3.9	2.9	2.9	<2.9	<2.8	<2.8	<2.8
III	10.0	8.8	8.8	10.8	5.8	5.8	4.8	4.8	4.8	4.8	4.2	4.2	3.8	3.8	3.9	3.9
IV	13.9	13.8	13.8	14.2	10.0	10.0	7.8	7.1	7.1	7.1	5.8	5.8	4.8	4.8	4.8	4.8
V	25.8	23.8	...	...	17.3	16.4	13.3	12.3	13.4	...	10.0	10.0	8.8	8.7	8.7	...
VI	28.9	28.4	...	...	19.9	18.0	15.7	14.3	13.8	...	11.7	11.4	9.6	9.2	8.8	...

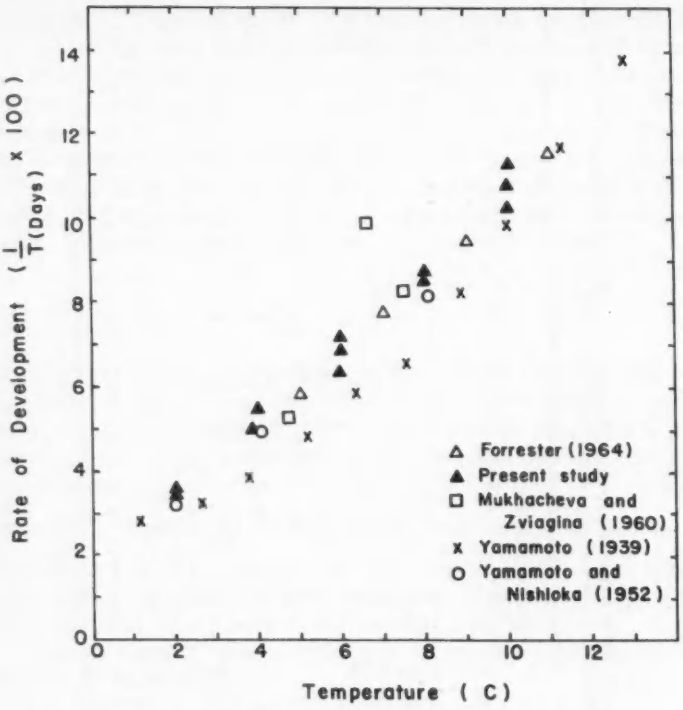

FIG. 2. Rate of development from fertilization to 50% hatch for Pacific cod eggs held at various temperatures.

DURATION OF HATCHING TIME

The duration of hatching time for each salinity-temperature combination is shown in Table III. These hatching intervals ranged from 36 hr at 10 C (31‰ S) to 246 hr at 2 C (25‰ S). There was, in general, an inverse relationship between both temperature and salinity with respect to the duration of the hatching period.

SIZE OF LARVAE

Larvae were sampled at intervals throughout the hatching period. In any one salinity-temperature combination a considerable variation in larval size was found at each sampling interval. Moreover, the trend in all cases was toward an increase in larval size throughout the hatching period. However, the distribution of larval sizes throughout the course of hatching in any one salinity-temperature combination followed several forms as illustrated in Fig. 4 (A, B) for larvae obtained at 19‰ S, 6 C and 25‰, 10 C, respectively. For these reasons it was difficult to assign standard measures of larval size

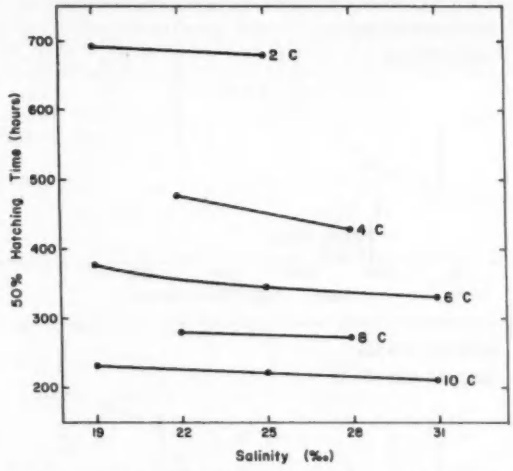

FIG. 3. Influence of salinity on the time to 50% hatch of Pacific cod eggs held at five constant temperatures from 2 to 10 C.

TABLE III. Duration of hatching in hours for Pacific cod eggs held at various constant salinity–temperature conditions.

Salinity ‰	Temperature(C)				
	2	4	6	8	10
19	193.5		167.5		98.0
22		166.0		110.0	
25	245.5		124.0		45.0
28		104.0		99.5	
31	...		89.5		36.0

for each condition investigated. The estimated size of larvae at the 50% hatching interval, as obtained from a plot of means of larval size at each sampling interval (Fig. 4), was virtually identical with the overall mean for all larvae sampled in each salinity–temperature condition (Table IV). In view of the close agreement between the two estimates of size, only the overall mean larval sizes are shown in Fig. 5. Largest larvae, on the average, were found in 6 C and 19‰ S. In general, however, there was an inverse relationship between size of larvae and salinity and temperature within the ranges investigated.

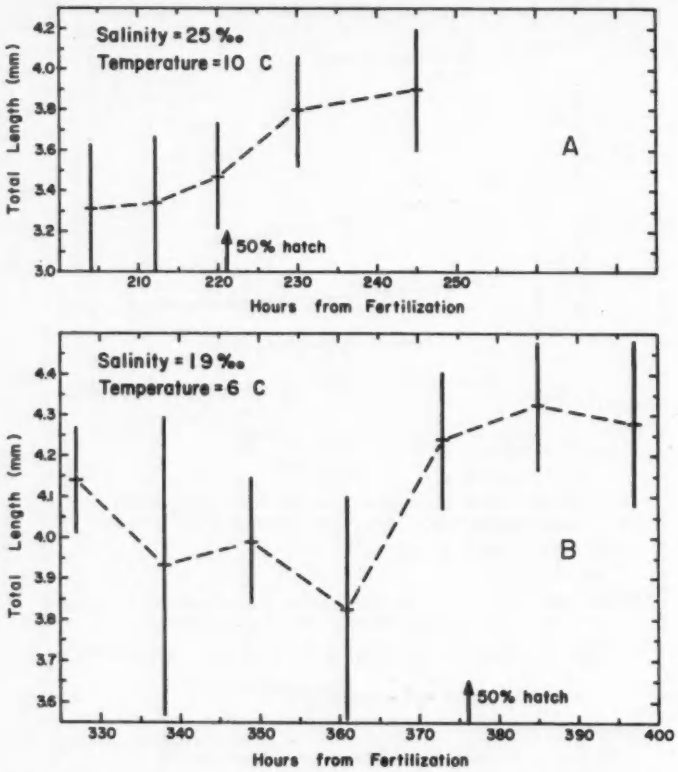

FIG. 4A, B. Differences in size of cod larvae sampled throughout the hatching interval. Two types of distributions are noted. (A) Those in which there is a progressive increase in mean size; and (B) those in which there is a decrease in larval size in the first part of the hatching interval. Mean larval size ± 1SD is shown for each sample taken.

HATCHING EFFICIENCY

Counts of live hatched larvae were obtained for each of the four subsamples of eggs in 13 test combinations of salinity and temperature. A more detailed analysis of the proportions hatching under the various experimental conditions was undertaken in order to estimate the relation of hatching success to salinity and temperature levels. The percentage hatch in each subsample of the 13 trials is listed in Table V.

There was considerable variation in hatching success within each trial. While an attempt was made to place approximately equal numbers of eggs in each container this was made difficult by the small size of the eggs (diam ca. 1 mm) and, to a lesser extent, their adhesive character. The mean and standard deviation of the number of eggs in all containers was 1704 ± 314

TABLE IV. Mean size of larvae (*mm*) at time of hatching. The figures in brackets refer to the estimated size of larvae at the time of 50% hatch.

Salinity ‰	Temperature (*C*)				
	2	4	6	8	10
19	4.10		4.16		3.75
	(4.11)		(4.21)		(3.76)
22		3.99		3.86	
		(4.00)		(3.92)	
25	4.13		3.86		3.52
	(4.09)		(3.92)		(3.51)
28		3.83		3.79	
		(3.65)[a]		(3.84)	

[a]Measurements of larvae from this test were made after the 50% hatching time and may be in error.

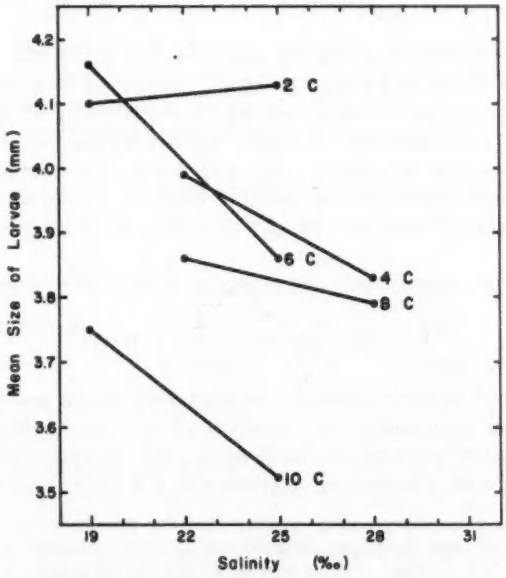

FIG. 5. Mean size of newly-hatched Pacific cod larvae incubated under constant salinity-temperature conditions.

TABLE V. Percentage of Pacific cod eggs producing live hatched larvae.

Trial	Salinity(‰)	Temperature(C)	Subsample 1	2	3	4
1	19	2	15.86	19.49	7.46	4.32
2	19	6	28.34	33.47	14.69	23.76
3	19	10	14.51	9.36	17.11	8.34
4	22	4	11.54	15.70	5.03	14.25
5	22	8	4.50	2.19	4.95	6.51
6	25	2	10.84	7.93	11.52	9.26
7	25	6	19.30	11.57	8.94	2.89
8	25	10	1.16	6.83	2.22	5.30
9	28	4	2.27	0.74	1.17	0.94
10	28	8	12.31	1.65	2.92	8.82
11	31	2	0.00	0.00	0.05	0.00
12	31	6	0.24	0.95	1.67	0.91
13	31	10	0.00	0.43	0.43	0.17

eggs while the smallest and largest samples contained 925 and 2561 eggs, respectively. In 11 out of 12 trials in which comparison was possible, hatching success appeared to be inversely related to the number of eggs in the containers. However, a possible correction applied to the proportion hatching, based on equalization of sample sizes, was considered of questionable value because of evident random error within trials and the small number of subsamples employed. Therefore, the decision was made to proceed using the basic data.

The analysis was carried out using a transformed dependent variable

$$U = \log (\text{per cent hatch} + 0.05).^3$$

The constant 0.05 approximates the smallest measurable per cent response in the experiments, equivalent to a survival of one egg in a sample of 2000. The transformation removes to a large extent the obvious association between mean and subsample variance apparent in the raw data. Furthermore, a more

[3]Computer runs were conducted using as the dependent variable: p, arcsin $(p)^{\frac{1}{2}}$, $(p)^{\frac{1}{2}}$, $(p + c)^{\frac{1}{2}}$ and $\log_{10}(p + c)$, where p = per cent survival to hatching and c = various constants. The transformation selected "explained" the largest portion of treatment variance in terms of the regression model.

sensitive measure of the effects of the treatments is provided by the transformed scale.

A preliminary analysis of variance shows that the subsample effect associated with the position of egg containers in the experimental tanks is very small and can be ignored, and that the treatment effects are highly significant when tested against the pooled error term.

Source of variance	Sum of squares	*df*	Mean square	Variance ratio
Treatments	27.74040	12	2.31170	29.558**
Residual (pooled)	3.05009	39	0.07821	
Subsample effect	0.01700	3	0.00567	0.067 N.S.
Treatment × sub-sample interaction	3.03309	36	0.08425	
Total:	30.79049	51		

**F.99 (12,39) = 2.68; *F.95 (3,36) = 2.86

In order to consider the regression of hatching success on salinity and temperature levels it was next assumed that a second order polynomial would provide an adequate fit to the data, where

$$U = b_0x_0 + b_1x_1 + b_2x_2 + b_{11}x_1^2 + b_{22}x_2^2 + b_{12}x_1x_2$$

x_1, x_2 = coded values for salinity and temperature (see Alderdice, 1963).

The treatment sum of squares next is partitioned into a component associated with total regression on x_1, x_2, x_1^2, x_2^2 and x_1x_2, and a component that could not be explained by regression on these factors.

Source of variance	Sum of squares	*df*	Mean square	Variance ratio
Treatments				
Total regression	24.26197	5	4.85239	62.043**
Deviations from regression	3.47843	7	0.49692	6.354**
Residual (pooled)	3.05009	39	0.07821	
Total:	30.79049	51		

**F.99 (5,39) = 3.53; F.99 (7,39) = 3.14

The five factors in the second degree polynomial account for 87.46% of the variability between treatments. The statistical significance of the deviations from regression indicates that one or more higher order terms exist. Partitioning of total regression sum of squares into the parts associated with

each term in the second degree polynomial shows that all terms except the linear effect of temperature are statistically significant.[4]

Source of variance	Sum of squares	*df*	Mean square	Variance ratio
x_1 (Salinity)	19.59870	1		250.591**
x_2 (Temperature)	0.03763	1		0.481
x_1^2 (S^2)	2.81484	1		35.991**
x_2^2 (T^2)	1.27439	1		16.294**
x_1x_2 (S × T)	0.53641	1		6.859*
Residual (pooled) error		39	0.07821	

**F.99 (1, 39) = 7.33; *F.95 (1,39) = 4.09

The fitted equation is

$$U = 0.93562 - 0.83663x_1 + 0.03666x_2 - 0.46181x_1^2 - 0.36529x_2^2 + 0.17763x_1x_2.$$

The regression of hatching success on salinity and temperature levels in these experiments could be described graphically from the above equation. For convenience, however, the polynomial was transformed to its equivalent canonical form. This transformation involves a translocation from the centre of the experimental design to the calculated centre of the response surface with reference to the effects of salinity and temperature on hatching success, and a rotation of the axes of the design to those of the response surface (Box, 1954, 1956).

Hence:

$$U - U_s = \lambda_{11}X_1^2 + \lambda_{22}X_2^2$$

where U_s = transformed per cent hatch estimated at the centre of the hatching surface, S

λ_{ii} = the rate at which the response changes in the direction of the X_i axes of the response surface.

By calculation, therefore,

$$U - 1.32562 = -1.681X_1^2 - 4.439\ X_2^2.$$

Furthermore, the locus of U_s is estimated by partial differentiation of the second degree polynomial and solution of the resulting equations (Box, 1956).

[4]The design employed in this study does not permit separation of linear and cubic terms (i.e. $\beta_1 \rightarrow b_1 + b_{111}$). The significance of the term for deviations from regression and the magnitude of the linear effect of salinity suggests the existence of a cubic term associated with the effects of salinity (x_1^3).

Converting to original terms, maximum hatching success is found at the centre of the response surface, at or in the vicinity of 19.4‰ S and 5.3 C.

From the procedures outlined, regression isopleths have been constructed in Fig. 6 representing several levels of expected per cent hatch with respect to salinity and temperature. Finally, the calculated temperatures at which maximum hatch could be expected with respect to salinity (within the range of 19 – 31‰ S) are presented in Fig. 7, which is based on the following values:

Salinity, (‰)	Temperature, (C)
19	5.2
22	5.7
25	6.2
28	6.7
31	7.2

The relationship in Fig. 7 indicates, with respect to salinity, the temperatures at which maximum per cent hatch would be expected if the studies had been

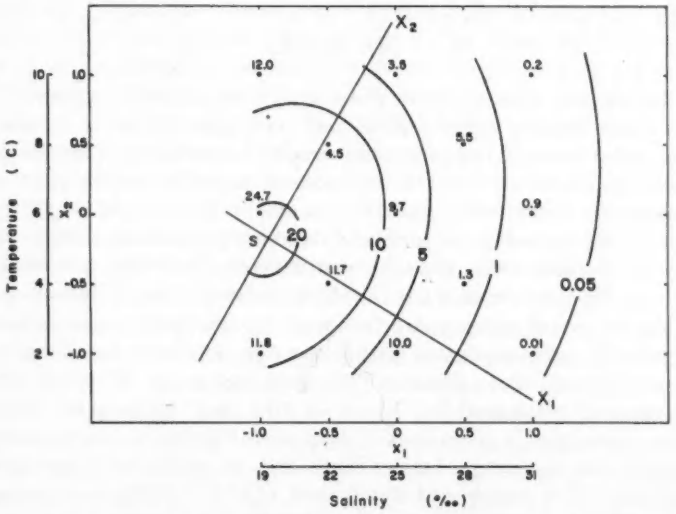

FIG. 6. Regression surface showing the relationship between salinity and temperature levels and hatching success. Hatching isopleths are shown at 0.05, 1, 5, 10, and 20% viable hatch as calculated from the regression equation. The X_1, X_2 axes, with centre S, are the geometric axes of the regression surface. Salinity and temperature levels calculated at S are 19.4‰ S and 5.3 C. The array of points in the figure locates the conditions of the experimental trials; the values shown in the array represent the observed mean per cent hatches for each trial.

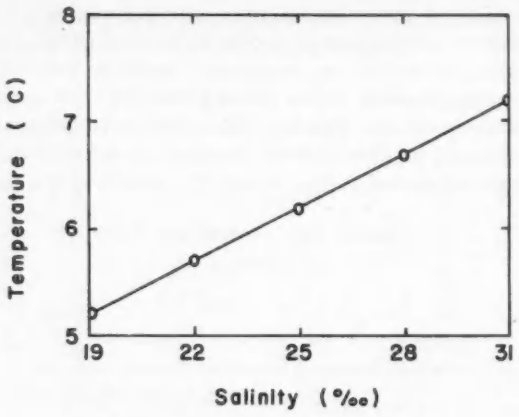

FIG. 7. Temperatures at which maximum hatching success would be expected with respect to salinity, as calculated from the regression surface.

carried out over a series of temperatures at several or more constant levels of salinity.

DISCUSSION

Of the various abiotic factors which may influence development of teleost eggs, undoubtedly the physiological and ecological effects of salinity, temperature and dissolved oxygen are of major importance. Temperature and dissolved oxygen affect the rate of gross embryonal development through their influence on metabolic rate (Hayes et al., 1951; Garside, 1959; Kinne and Kinne, 1962) as well as on form and structure of resulting larvae (Alderdice et al., 1958; Garside, 1959; Holliday and Blaxter, 1960; Blaxter and Hempel, 1961; Kinne, 1963; Silver et al., 1963; Shumway et al., 1964; Sweet and Kinne, 1964). The effects of salinity are less well documented but presumably are associated with osmo-regulation within the egg (Holliday and Blaxter, 1960; Prosser and Brown, 1961; Kinne, 1964). Pertinent to the following discussion is the argument advanced by Kinne (1963) that "in general, the osmo-regulative capacity of a given species appears to be greatest at near-optimum temperatures or somewhat below that, and to decrease in supra-normal temperatures." The response of Pacific cod eggs to salinity and temperature will be considered with respect to this postulate.

In the present study, consideration was placed on aspects of development and survival as influenced by salinity and temperature only. Experimental conditions were set up, therefore, on the premise that oxygen could be maintained at sufficiently high concentrations to provide independence of response over oxygen level. However, the ensuing inverse relationship noted between

number of eggs per subsample and resulting live hatch suggests that independence of oxygen level was not achieved. The observations attributable to the effects of salinity and temperature are subject, therefore, to a possible bias resulting from suspected hypoxial conditions in the incubation containers. This possibility will be considered in the ensuing discussion.

Rate of Development

An hyperbolic relationship is suggested between temperature and time for all six developmental stages considered (Fig. 1). Moreover, rate of development to 50% hatch is an approximate linear function of temperature within the 2–10 C range considered. There is good agreement between the present results and most other studies on *G. macrocephalus* with which they are compared (Fig. 2).

In the present case a slight but consistent retardation in rate of development was associated with reduction of salinities at each temperature level examined (Table II). Comparisons made regarding the effects of salinity on rate of development of other species lead only to the conclusion that there are many species-dependent patterns of response (Kinne, 1963). Effects of salinity on rate of development may simulate those resulting from low ambient dissolved oxygen. Kinne and Kinne (1962) demonstrated in the case of the desert pupfish (*Cyprinodon macularius*[5]) that a delay in hatching associated with the lower availability of dissolved oxygen in higher salinities could be eliminated by oxygenating the incubation medium to provide oxygen levels above saturation. Delayed development from hypoxia is well known in the incubation of salmonid eggs (Garside, 1959). In the present case, however, incubation periods are shorter in higher salinity levels. If lower ambient oxygen levels in higher salinities should increase incubation time, the difference between length of incubation period in low and high salinities would then be proportionately diminished. It is suggested, therefore, that the relationship indicated between salinity and development time may have been modified but not governed by ambient oxygen level over the salinity range employed.

Data on the rate of development of *G. macrocephalus* as a function of temperature is compared in Fig. 8 with similar evidence for *G. morhua*[6] (see Appendix Table I). Considerable scatter is evident in the data compared, presumably associated in part with variation in experimental conditions. The effect of temperature on rate of development, however, appears to be quite similar for the two species. The more extensive data for *morhua* at low temperatures

[5]Although *macularius* is listed as a freshwater species (Anon, 1960) it is holoeuryhaline and may exist in environments from fresh water to salinities equal to or considerably greater than oceanic salinities (Kinne, 1960).

[6]Rate of development of Pacific and Atlantic cod eggs is compared here without reference to the systematic relationship between the two species. Systematics of the genus *Gadus* are subject to conjecture (for a discussion see Ketchen, 1961). In Canadian waters *macrocephalus* has a demersal egg but elsewhere opinion on specific gravity of eggs of this species is in debate (Thomson, 1963). *Gadus morhua* has a pelagic or near pelagic egg (Wise, 1958) depending mainly on the salinity characteristics of its environment.

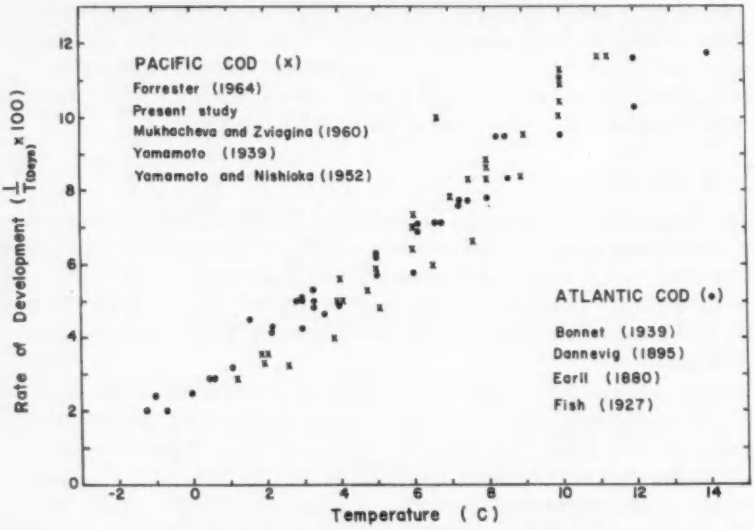

FIG. 8. Comparison of data on rate of development as affected by temperature for eggs of the Pacific and Atlantic cod.

suggests for this species, and perhaps for *macrocephalus*, that the relationship between temperature and rate may in fact be curvilinear. Based on present findings, estimates of developmental rates below 2 C for *macrocephalus* would most likely be achieved in waters of low salinity (Fig. 6).

SIZE OF LARVAE

Inspection of Table IV indicates that largest larvae were obtained in the 19‰ S, 6 C incubation test. However, if larval size is considered in terms of a plane in salinity and temperature (Table IV), there is a suggested ridge system in larval size similar to that found for hatching efficiency (Fig. 6). In this respect the data suggest that maximum larval size may be associated with those salinity and temperature conditions which produce maximum survival to hatching. In general, Pacific cod larvae appear to hatch at larger sizes in lower temperatures and salinities, observations consistent with those of Kinne and Kinne (1962) for the desert pupfish, and Holliday and Blaxter (1960), Blaxter and Hempel (1961) for the Atlantic herring (*Clupea harengus*).

HATCHING EFFICIENCY

The regression plane illustrated in Fig. 6 is indicative of a rather broad tolerance of incubating cod eggs to various salinity levels. Surprisingly, success of hatching was lowest in the higher salinities including those approximating conditions for the spawning area from which the eggs were taken (29–30‰ S;

(M. Waldichuk, personal communication). Success of hatching appears to increase in lower salinities to a maximum *calculated* at about 19.4‰ S and 5.3 C.

It is also apparent that salinity and temperature are not independent of one another in their action on hatching success. The interaction between the two factors is implied in the rotation of the X axes with respect to the salinity and temperature (x_1, x_2) axes in Fig. 6. This being so, no single "optimal" value for salinity and temperature can be stated within the range of conditions expected in the natural environment. Rather, a range of optimal values would result, as estimated and illustrated in Fig. 7.

As noted earlier the possibility exists that salinity and temperature effects may have been biased by hypoxial conditions in the incubation containers. The manner in which this possibility may have affected hatching efficiency may be reviewed in two ways. First, there may be an interaction between effects of salinity and/or temperature with those of dissolved oxygen. Under such conditions temperatures at which maximum hatch occurred would be shifted from their true position. Such a shift presumably would be in the direction of lower temperatures where lower development rates would allow eggs to continue respiring. The trend of the present data is indistinguishable from that of other available data presented in Fig. 2, suggesting that dissolved oxygen has not biased rate of development at any temperature. Another possible effect of hypoxia might be a depression of hatching efficiency at all salinity and temperature conditions without alteration of the general shape of the hatching surface (Fig. 6). This possibility is supported by the relatively small hatches obtained in all test conditions, and is further supported by a comparison of hatching success obtained by Forrester (1964) with one test of the present series. At 26.5‰ S and 5 C he obtained about 23% survival whereas a comparable test in this series (25‰ S, 6 C) produced 10% survival. It is tentatively concluded that eggs in this study were subjected to hypoxia, resulting in a depression of survival rates over all experimental combinations.

Combined Effects of Salinity and Temperature on Egg Development

If osmo-regulation is most efficient at or just below the optimal temperature for development, least osmotic stress would be expected in the present case at or near 19.4‰ S. At this salinity one would anticipate a lengthened incubation period. In a similar case Holliday and Blaxter (1960) incubated Atlantic herring eggs at various salinities and found the incubation period was 2 days longer (13 days) at 5.9 and 11.5‰ S than at salinities of 22.7 and 52.5‰. On the other hand, McMynn and Hoar (1953) noted that rate of development of Pacific herring (*Clupea pallasii*) eggs was the same in salinities ranging from 6.06 to 34.28‰ (at 7 C). These authors suggest on the basis of egg survival, however, that osmotic stress is likely minimal at isotonic salinities, probably within the range of 11.55–16.24‰ S. Blaxter and Hempel (1961) obtained maximum size of newly-hatched Atlantic herring larvae at

15‰ S (8 C), a salinity they considered to provide isotonic conditions. They also noted that yolk contents were smallest in newly-hatched larvae between approximately 5–15‰ S. In the case of Pacific cod least osmotic stress may be associated with low salinities (19–21‰) at temperatures of 5–7 C, conditions under which both larval size and survival to hatching appear to be maximal.

The experimental evidence suggests that salinity and temperature have approximately the same influence on hatching success within the salinity–temperature region investigated. Changes of 1 C appear equivalent in effect on hatching success to a change of about 1.2‰ S. The interacting effects of the two environmental factors emphasize the obvious need for consideration of both salinity and temperature in studies of development in *G. macrocephalus*.

SUMMARY

1. Fertilized eggs of the Pacific cod (*Gadus macrocephalus*) were held to completion of hatching in various combinations of constant salinity (19‰–31‰) and constant temperature (2–10 C).
2. Development to hatching occurred in all salinities and all temperatures. Survival to hatching was highest at the lower levels of these factors.
3. Development time (to 50% hatching) ranged from approximately 8.8 days at 10 C (31‰ S) to 28.9 days at 2 C (19‰ S).
4. Rate of development (the reciprocal of time in days to 50% hatch × 100) was found to be directly related to temperature and the relationship was closely linear for temperatures of 4–10 C with a suggested departure from linearity below 4 C.
5. At all temperatures development time (to 50% hatching) appeared to be "delayed" by reduction in salinity.
6. The eggs used in this study were probably subjected to hypoxial conditions. The most probable result of this condition is suspected as a depression of survival to hatching over all experimental combinations of salinity and temperature.
7. Duration of the hatching period ranged from 36 hr at 10 C (31‰ S) to 246 hr at 2 C (25‰ S). There was, in general, an inverse relationship between both salinity and temperature with respect to the duration of hatching.
8. Mean larval size at time of hatching ranged from 3.52 mm (10 C, 25‰ S) to 4.16 mm (6 C, 19‰ S). There appeared to be an inverse relationship between salinity and temperature, and size of larvae. Larval size in these experiments would appear to be maximal in the vicinity of 19‰ S and 5 C.
9. Response isopleths calculated from the present experimental data suggest maximum hatching success may be found in the vicinity of about 19.4‰ S and 5.3 C. A significant interaction was found between the effects of salinity and temperature on development. The *calculated* temperatures at which maximum hatch could be expected with respect to salinity, within the range of 19 to 31‰ are:

Salinity, (‰)	Temperature, (C)
19	5.2
22	5.7
25	6.2
28	6.7
31	7.2

10. The response isopleths suggest that eggs of *G. macrocephalus* are euryhaline. Changes of 1 C were calculated to be equivalent in effect on hatching success to a change of about 1.2‰ S.

ACKNOWLEDGMENTS

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APPENDIX TABLE I. Summary of information on rate of development of Pacific and Atlantic cod used in Fig. 8. Incubation temperatures shown in the table are in most cases averages of temperature ranges (in brackets) from the original papers.

Pacific cod				Atlantic cod			
Incubation time, *days*	Rate of development	Temp	Reference	Incubation time, *days*	Rate of development	Temp	Reference
(T)	$\left(\frac{1}{T} = 100\right)$	*C*		(T)	$\left(\frac{1}{T} \times 100\right)$	*C*	
7.2	14.0	12.8	Yamamoto (1939)	13	7.7	7.2	Earll (1880)
8.5	11.8	11.3	"	16	6.3	5.0	"
10.0	10.0	9.9	"	20	5.0	3.3	"
12.0	8.3	8.9	"	24	4.2	2.2	"
15.1	6.6	7.6	"	31	3.2	1.1	"
16.8	6.0	6.4	"	34	2.9	0.6	"
21.0	4.8	5.2	"	50	2.0	−0.6	"
25.2	4.0	3.8	"	42	2.4	−1.0	Dannevig (1895)
30.6	3.3	2.7	"	23	4.3	3	"
35.3	2.8	1.2	"	20.5	4.9	4	"
12	8.3	8	Yamamoto and	17.5	5.7	5	"
		(6–10)	Nishioka (1952)	15.5	6.5	6	"
20	5.0	4		12.8	7.8	8	"
		(3–6)	"	10.5	9.5	10	"
30	3.3	2		9.7	10.3	12	"
		(1.5–2.5)	"	8.5	11.8	14	"

(*continued*)

APPENDIX TABLE I. (*Concluded*)

Pacific cod				Atlantic cod			
Incubation time, *days*	Rate of development	Temp	Reference	Incubation time, *days*	Rate of development	Temp	Reference
19	5.3	4.75 (4.0–5.5)	Summarized in Mukhacheva and Zviagina (1960)	13	9.5	8.50	Fish (1927)
				12	8.3	8.56	"
12	8.3	7.5 (6.0–9.0)	"	14	7.1	6.8	"
				14	7.1	6.67	"
10	10.0	6.7 (6.3–7.0)	"	20	5.0	2.83	"
				22	4.5	1.56	"
8.6	11.6	11	Forrester (1964)	19	5.3	3.33	"
10.5	9.5	9	"	10.5	9.5	8.33	Summarized in Fish (1927)
12.8	7.8	7	"	13	7.7	7.50	"
16.9	5.9	5	"	14	7.1	6.11	"
8.8	11.3	10	This paper	14.5	6.9	6.11	"
9.2	10.9	10	"	16	6.3	5.00	"
9.6	10.4	10	"	20	5.0	3.33	"
11.4	8.8	8	"	20	5.0	3.00	"
11.7	8.6	8	"	21.5	4.7	3.61	"
13.8	7.3	6	"	21	4.8	3.33	"
14.3	7.0	6	"	24	4.2	2.20	"
15.7	6.4	6	"	34	2.9	0.50	"
18.0	5.6	4	"	40 or more	2.5	0.00	"
19.9	5.0	4	"	50	2.0	−1.20	"
28.4	3.5	2	"	17.2	5.8	6	Bonnet (1939)
28.9	3.5	2	"	11.5	8.7	8	"
				9.0	11.1	10	"
				8.5	11.8	12	"

Swimming Endurance of Some Northwest Atlantic Fishes[1]

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ABSTRACT

Endurance was determined in relation to swimming speed and temperature for Atlantic cod, *Gadus morhua* Linnaeus, redfish, *Sebastes marinus* (Linnaeus), winter flounder, *Pseudopleuronectes americanus* (Walbaum), and to swimming speed at 8 C for longhorn sculpin, *Myoxocephalus octodecimspinosus* (Mitchill), sea raven, *Hemitripterus americanus* (Gmelin), and ocean pout, *Macrozoarces americanus* (Block and Schneider).

In an activity chamber at a swimming speed of 4 body lengths per second (BL/sec) Atlantic cod swam for about equally long periods at 5 and 8 C, and redfish and winter flounder each about equally long at 5, 8, and 11 C. The pattern was similar for higher speeds. At 14 C winter flounder swam longer at 6 BL/sec than at the lower temperatures. For swimming speeds less than 4 BL/sec all species swam longer at the higher temperatures. At 8 C, the only temperature at which all species were tested, endurance at comparable swimming speeds was greatest for winter flounder, followed by cod, redfish, longhorn sculpin, ocean pout, and sea raven.

INTRODUCTION

Endurance was measured in relation to swimming speed and temperature for three commercially important species, Atlantic cod, *Gadus morhua* Linnaeus, redfish, *Sebastes marinus* (Linnaeus) and winter flounder, *Pseudopleuronectes americanus* (Walbaum). Longhorn sculpin, *Myoxocephalus octodecimspinosus* (Mitchill), sea raven, *Hemitripterus americanus* (Gmelin), and ocean pout, *Macrozoarces americanus* (Block and Schneider), were also studied; these are common in northwestern Atlantic otter-trawl catches but are not yet of commercial importance.

Cod were used as a yardstick for comparison with the findings by European investigators (Blaxter and Dickson, 1959; Sundnes, 1963) for fish from the northeastern Atlantic. Although redfish occur in eastern and western Atlantic waters, there is no published information on their swimming performance. Endurance of winter flounder of the northwestern Atlantic has not been reported previously.

Swimming endurance of fish in relation to swimming speed is important in avoidance of towed nets and may assist in the design of fishing gear. The only detailed information on swimming speeds for northwestern Atlantic fishes is given in Brawn's (1960) and Boyar's (1961) work on Atlantic herring, *Clupea harengus harengus* Linnaeus, from the Bay of Fundy.

For fish of the northeastern Atlantic swimming speeds have been determined (Magnan, 1930; Blaxter and Dickson, 1959; Sundnes, 1963) for many species,

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some of which occur also on the western coast. These include Atlantic cod, haddock, *Melanogrammus aeglefinus* (Linnaeus), pollock, *Pollachius virens* (Linnaeus), Atlantic mackerel, *Scomber scombrus* Linnaeus, and Atlantic herring.

MATERIALS AND METHODS

All species except redfish were captured by otter trawl at depths between 45 and 60 m. After capture, the fish were held alive in tanks aboard the research vessel M. B. *Mallotus* until taken to the laboratory and transferred to circular holding tanks (diam 2 m, depth 1.5 m).

The opportunity to work with redfish in a laboratory was unique. Generally this species is found in deep water and does not survive when brought to the surface. However, a stock frequents the pilings and wharves off Eastport, Maine, in Passamaquoddy Bay. Experimental animals were captured there by barbless hooks.

All species were maintained on a diet of herring and beef liver.

In all experiments fish were first acclimated to a particular temperature by allowing a change of 1 C per day until the desired temperature was reached. They were then held at this temperature for at least a week before testing. Winter flounder were tested at 5, 8, 11, and 14 C, redfish at 5, 8, and 11 C, cod at 5 and 8 C, and the other species at 8 C. These temperatures represent the upper halves of the ranges at which the fish are found. Oxygen levels were maintained at air saturation.

Swimming endurance was determined in an activity chamber (Fig. 1) built after that described by Blazka et al. (1960). Blazka et al. (1960) needed a closed system in their metabolic studies. But for endurance measurements an open system was more fitting. Hence a cylindrical lucite chamber was immersed in an open bath, appropriately baffled at either end. A wooden cover for the

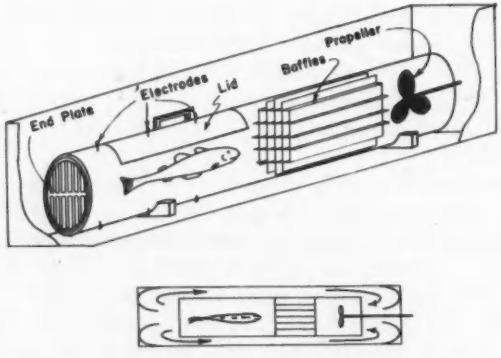

FIG. 1. Activity chamber, illustrating design and direction of flow. Length of the cylinder is 107 cm and the inner diameter 16.5 cm. The length of chamber available to a fish is 65 cm.

bath reduced splashing. Water velocity in the chamber was regulated by speed of a propeller which was driven by a variable-speed ¾-hp motor. Maximum water velocity in the chamber was 135 cm/sec. Water passed through the chamber, entered the bath and returned to the propeller end of the chamber as shown by arrows in Fig. 1. Baffles in the cylinder promoted laminar flow. A perforated end plate permitted water passage but prevented escape of fish. A lid on the chamber allowed insertion and removal of fish. Three pairs of electrodes provided mild stimuli (6 v) when necessary. Water velocity was measured with an Ott current meter (model Arkansas).

Fish to be tested were placed in an activity chamber 15 min prior to a run. To begin an experiment, water velocity was slowly but steadily increased to the desired speed. Gentle prodding was used sometimes, and electrical stimuli less often, to induce fish to swim. When a fish was fatigued, it was forced against the end plate. Usually the onset of fatigue was obvious. Swimming endurance was measured as the time a fish maintained its position against a current of known velocity. It was assumed that swimming speed was equal to water velocity. Generally, fish were not allowed to swim for more than 4 hr. When endurance lasted 4 hr, it was recorded as continuous swimming. After a run the fish was removed, weighed and measured. Each fish was used only once. Whenever practicable, 10 fish were used at each water velocity and, for each species, fish of similar size were selected. All species except cod were starved for 48 hr prior to testing. Cod received rations to the day of an experiment.

Standard error of the mean was calculated, as outlined in Stanley (1960), for weight, length, and endurance for each experiment.

RESULTS

Endurance of cod decreased sharply with increased swimming speed. The fish swam for more than 4 hr at a swimming speed of 75 cm/sec at both 5 and 8 C (Table I). At 5 C endurance was 12 min against a flow of 90 cm/sec, and decreased to about 4 min at 135 cm/sec. At 8 C, the corresponding endurances were continuous (more than 4 hr) and just over 5 min.

Endurance of redfish also decreased sharply with increased swimming speed. At 5 and 8 C (Table I), redfish swam 14 min at 52 cm/sec and less than 1 min at 135 cm/sec. At 11 C, they swam continuously at 52 cm/sec but less than 1 min at 135 cm/sec. Of the several fish tested at 45 cm/sec and 8 C (not shown in Table I), one was still swimming at 170 hr and two others at 40 hr when the experiments were stopped. At 5 and 8 C there was no appreciable difference between endurances for corresponding speeds (Table I). At 11 C, redfish swam much longer at 52 and 60 cm/sec than at 75 through 135 cm/sec, and at the latter speeds endurances were not significantly different from those at 5 and 8 C.

Winter flounder could not be induced to swim at speeds less than 75 cm/sec. Above this, they swam well, although endurance decreased rapidly with increase

TABLE I. Average swimming endurances of three species at various water velocities and temperatures.

Species	Temp.	Swimming speed	Weight ± SE	Length ± SE	Endurance ± SE
	C	*cm/sec*	g	*cm*	*min*
Cod	8	75[a]	600±45	35.3±0.8	[b]
		90	520±39	35.0±0.8	[b]
		105	572±54	36.0±0.8	16.4±5.1
		135	526±63	35.2±0.9	5.6±1.6
	5	75	586±60	36.1±0.7	[b]
		90	529±42	35.5±0.7	11.7±1.2
		105	581+52	35.3±1.0	6.1±1.1
		135	635±62	36.5±0.8	4.2±1.0
Redfish	11	52	139±19	17.2±0.7	[b]
		60	121± 9	16.9±0.4	12.7±6.1
		75	137±20	17.2±0.9	4.6±0.7
		90	136±22	16.9±0.9	2.7±0.3
		105	115±12	16.4±0.6	1.5±0.2
		120	114±13	16.1±0.6	0.8±0.1
		135	140±17	17.2±0.8	0.6±0.1
	8	52	113± 8	15.9±0.4	13.2±2.5
		75	137±19	17.1±0.8	2.7±0.3
		105	137±14	17.2±0.6	1.7±0.3
		135	135±17	17.0±0.6	0.8±0.1
	5	52	132±14	17.3±0.6	14.2±3.0
		75	131±14	17.4±0.8	3.0±0.5
		105	166±21	18.6±0.8	1.5±0.2
		135	127±20	16.9±0.8	0.7±0.1
Winter flounder	14	75	215± 3	23.1±0.7	25.4±3.3
		135	219±15	22.3±0.9	5.3±1.2
	11	75	136± 9	19.1±0.4	10.0±1.2
		105	130± 9	18.9±0.3	3.2±0.4
		135	171±20	20.4±0.2	1.4±0.2
	8	75	190±22	21.0±0.7	10.3±1.0
		105	149±22	19.4±0.4	5.8±0.7
		135	178±20	20.6±0.8	1.7±0.2
	5	75	135± 9	19.0±0.3	14.1±1.5
		105	149±15	19.5±0.6	5.8±0.6
		135	193±18	20.8±0.5	1.9±0.3

[a]Four fish used; in all other tests, 10.
[b]For more than 4 hr.

in swimming speed. At 5 C it dropped from 14 min at 75 cm/sec to less than 2 min at 135 cm/sec (Table I). There was little difference in endurance at 5, 8, and 11 C for comparable speeds except at 105 cm/sec, where flounder at 8 C swam longer than those at 5 or 11 C. At 14 C, endurances were considerably greater than those at the lower temperatures.

Swimming time of longhorn sculpin decreased from about 6 to less than ½ min between 60 and 120 cm/sec (Table II). When water velocity was less than 60 cm/sec, sculpins swam only for short bursts.

Endurance of ocean pout dropped markedly from just over 6 to approximately 1 min between 90 and 120 cm/sec (Table II). At lower velocities ocean pout could not be induced to swim.

TABLE II. Average swimming endurances of three species against various water velocities at 8 C.

Species	No. of fish	Swimming speed	Weight ± SE	Length ± SE	Endurance ± SE
		cm/sec	*g*	*cm*	*min*
Longhorn	10	60	156±18	21.1±0.9	6.7±0.9
sculpin	10	75	162±10	21.3±0.4	3.4±0.6
	10	90	152±10	21.1±0.4	1.3±0.2
	10	105	130±14	19.8±0.6	0.7±0.1
	10	120	134±12	19.8±0.6	0.5
Ocean pout	3	90	237±30	37.9±1.5	6.6±1.6
	4	105	156±16	33.6±1.0	1.6±0.2
	5	120	226±21	38.4±1.5	1.1±0.4
Sea raven	10	105	271±42	22.7±0.6	0.7±0.1
	6	120	234±87	18.8±1.9	0.4

Sea ravens swam less than 1 min at both 105 and 120 cm/sec (Table II). However, at the slower speed endurance (41 sec) was twice that at the faster speed (21 sec).

DISCUSSION

The findings that cod and redfish each swam for about equally long periods at the highest swimming speeds regardless of temperature (Table I) are in accord with the observations of Blaxter and Dickson (1959). They did not find any correlation between high swimming speed and temperature for plaice, *Pleuronectes platessa*, goldfish, *Carassius auratus*, brown trout, *Salmo trutta*, and blenny, *Zoarces viviparus*. Over the lower speeds for cod, redfish, and winter flounder, there is a suggestion of greater endurance with increased temperature. Endurance did not always increase with each increment of temperature; for example, endurances of redfish at low velocities did not differ appreciably at 5 and 8 C, but were higher at 11 C. Fry and Hart (1948) found with temperature increases between 5 and 20 C that the swimming speed which goldfish would maintain for 20 min increased. Brett et al. (1958) found similar relationships for young sockeye, *Oncorhynchus kisutch*, and coho, *O. nerka*, salmon, while Gibson and Fry (1954) reported the same pattern for lake trout.

To compare endurances of different size fish, swimming speeds were calculated as body lengths per second (BL/sec) as suggested by Bainbridge (1958). At 3.9 BL/sec, the highest speed at which cod were tested, their endurance ranged from 4 min at 5 C to over 5 min at 8 C (Fig. 2). At the same speed in body lengths per second, winter flounder swam 10–17 min, depending on

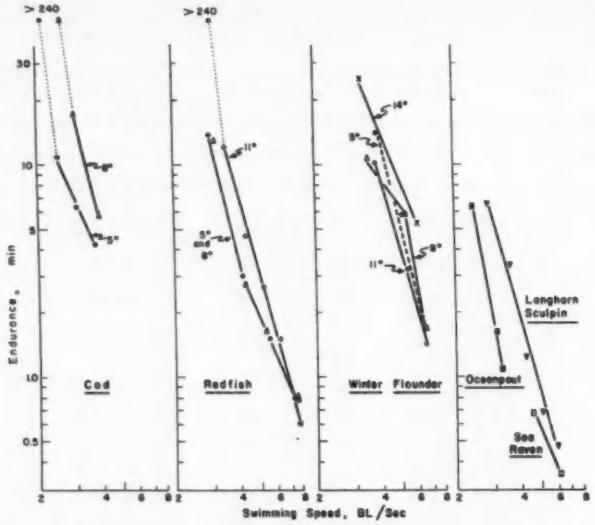

FIG. 2. Swimming endurances of six species calculated on basis of swimming speed in body lengths per second. Where endurance was more than 240 min it was taken as continuous. Broken lines connect continuous swimming with endurances of under 240 min.

temperature (Fig. 2, by interpolation), and redfish, 5 min at 5 and 8 C and 10 min at 11 C. Endurance of longhorn sculpin was just over 2 min (Fig. 2, by interpolation), and that of ocean pout and sea raven less than 1 min (Fig. 2, by extrapolation). At 6 BL/sec, winter flounder swam over 2 min, the longest endurance of the species tested. Redfish lasted between 1 and 2 min, considerably longer than the $\frac{1}{2}$ min swum by longhorn sculpin and sea raven.

Only redfish and winter flounder were tested above 6 BL/sec. Winter flounder lasted about $1\frac{1}{2}$ min at 6.7 BL/sec. Redfish swam for approximately 50 sec at 8 BL/sec before fatiguing. These values fall short of the limit suggested by Bainbridge (1958). He maintains that fish should be able to sustain 10 BL/sec for short periods of about 1 min. Indeed, extrapolation of the relations between endurance and swimming speed in Fig. 2 suggests none of the species could withstand 10 BL/sec for more than 30 sec.

However, the results do suggest greater endurances than those reported for similar swimming speeds. For a 50-cm cod, Blaxter and Dickson (1959) found endurance less than 1 min at about 3 BL/sec — considerably less than in this study. Sundnes (1963), on the basis of measurements of hydrodynamic drag and energy available for activity, calculated that a 113-cm cod could swim for 2 min at a speed of 2.2 BL/sec. The temperature on which calculations were made was not reported. Nevertheless, this is remarkably less than in the present investigation. At similar swimming speed, endurance was estimated by extrapolation as 14 min at 5 C and more than 4 hr at 8 C.

No information on swimming performance could be found in the literature for the other species used. However, both Sundnes (1963) and Blaxter and Dickson (1959) determined swimming speeds for flatfish other than winter flounder. Sundnes (1963) calculated that a 54-cm plaice, *Pleuronectes platessa*, could last just over 1 min at 4.4 BL/sec. At the same velocity, a 20-cm winter flounder swam up to 11 min, depending on the temperature. Maximum swimming speeds of approximately 4 BL/sec for small plaice and 5.2 BL/sec for large fish were recorded by Blaxter and Dickson (1959). Further, they recorded a maximum of about 4 BL/sec for *P. flesus* and 1.3 BL/sec for the one small *P. limanda* used, although endurances at these velocities were not reported.

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Exploitation in a Type of Predator–Prey Relationship[1]

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ABSTRACT

The properties are explored of the response to exploitation of the predator–prey system defined by the equations:

$$\frac{dN_1}{dt} = (r_1 - a_1N_1 - b_1N_2)\,N_1$$

$$\frac{dN_2}{dt} = (r_2 - a_2N_2 + b_2N_1)\,N_2$$

This type of equation is perhaps a suitable representation of the type of natural situation in which a predator (N_2) is not wholly dependent on one species of prey (N_1) for food, and in which factors other than predators may regulate prey abundance. Yield- and value-isopleths are presented for sample values of the above parameters and for various rates of fishing.

In community associations of fish species it is common to observe that predators consume a variety of prey species and that prey share a variety of predators. Thus only to a degree is there a mutual dependence of the abundance of a particular predator and a particular prey. For this reason, several of the variants of the familiar Lotka-Volterra equations seem inappropriate as associative models for describing predator–prey interactions amongst fishes. For example the Volterra model (D'Ancona, 1954):

$$\left.\begin{aligned}\frac{dN_1}{dt} &= (r_1 - b_1N_2)\,N_1\\ \frac{dN_2}{dt} &= (-d_2 + b_2N_1)\,N_2\end{aligned}\right\} \qquad (1)$$

has been the subject of frequent criticism, in part because the predator becomes extinct in the absence of its prey. There is no implied intraspecific competition for either the predator or the prey.

Kostitzin (1939, p. 131), in considering many variants of the Volterra equations, suggested the model:

$$\left.\begin{aligned}\frac{dN_1}{dt} &= (r_1 - a_1N_1 - b_1N_2)\,N_1\\ \frac{dN_2}{dt} &= (-r_2 - a_2N_2 + b_2N_1)\,N_2\end{aligned}\right\} \qquad (2)$$

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This set of equations includes provision for population regulation of the prey in the absence of the predator ($-a_1N_1^2$) and for intraspecific competition amongst the predators ($-a_2N_2^2$). It does not, however, suggest any alternative but extinction for the predator in the absence of prey. These equations were recently considered by Doi (1962) in analogue computer simulations of predator–prey relationships, but were abandoned in favour of equations (1) because of the inadequacy of his machine for handling the squared terms.

The modification of Leslie (1948) provided an appropriate machinery for partially meeting the criticisms of equations (1) and (2):

$$\left.\begin{aligned} \frac{dN_1}{dt} &= (r_1 - a_1N_1 - b_1N_2)\ N_1 \\ \frac{dN_2}{dt} &= \left(r_2 - b_2\frac{N_2}{N_1}\right) N_2 \end{aligned}\right\} \qquad (3)$$

In this system, the predator population tends to be regulated between limits, extinction being less probable because of the dependence of the rate of decline on the ratio of predators to prey.

None of these systems implies that the predator has alternate sources of food, which prevent extinction in the absence of prey, although such a situation seems commonplace in nature.

The present paper concerns a variation on these familiar themes, a model which seems appropriate for describing interactions between species of fish, where (a) the abundance of predator (N_2) and prey (N_1) are mutually dependent, (b) the abundance of the prey has an upper limit in the absence of the predator, (c) the abundance of the predator has a lower limit in the absence of the prey. Thus, for the predator, all of the factors of the environment other than the prey species are depicted by the parameter a_2 which summarizes the capacity of the environment to support predators in the absence of the particular prey N_1. Similarly for the prey, the value a_1 depicts population regulation by factors other than the predator in question. The equations are:

$$\left.\begin{aligned} \frac{dN_1}{dt} &= (r_1 - a_1N_1 - b_1N_2)\ N_1 \\ \frac{dN_2}{dt} &= (r_2 - a_2N_2 + b_2N_1)\ N_2 \end{aligned}\right\} \qquad (4A)^2$$

$$\left.\begin{aligned} \frac{dW_1}{dt} &= (r_1 - a_1W_1 - b_1W_2)\ W_1 \\ \frac{dW_2}{dt} &= (r_2 - a_2W_2 + b_2W_1)\ W_2 \end{aligned}\right\} \qquad (4B)$$

where species 1 is the prey and species 2 is the predator

[2]Alternatively the equations may be written in terms of weights of the predator (W_2) and prey (W_1) populations:

r_1 and r_2 are the intrinsic rates of natural increase

a_1 and a_2 are the coefficients of intraspecific competition

b_1 and b_2 are the coefficients, with respect to the other species, of decrease (prey) and increase (predator)

N_1 and N_2 are the numbers of prey and predator, respectively.

A system of equations which incorporated this representation of predation was among the suggestions of Kostitzin (1939, p. 114) and was intended as a depiction of the predation of whelks on mussels. Factors other than the abundance of mussels, or an alternate prey, barnacles, were also involved in regulation of the size of the whelk population.

The properties of the system described by equations (4A) may be explored in comparable fashion to those for competition as in Larkin (1963). In part, these have been presented in unpublished form by Dowidar (MS, 1963).

At equilibrium:

$$\left.\begin{aligned} N_1 = L_1 &= \frac{a_2 r_1 - b_1 r_2}{a_1 a_2 + b_1 b_2} \\ N_2 = L_2 &= \frac{a_1 r_2 + b_2 r_1}{a_1 a_2 + b_1 b_2} \end{aligned}\right\} \qquad (5)$$

Fixed percentage exploitation may be represented by adding the parameters c_i to equations (4):

$$\left.\begin{aligned} \frac{dN_1}{dt} &= (r_1 - c_1 - a_1 N_1 - b_1 N_2)\, N_1 \\ \frac{dN_2}{dt} &= (r_2 - c_2 - a_2 N_2 + b_2 N_1)\, N_2 \end{aligned}\right\} \qquad (6)$$

Displacements of equilibrium associated with various levels of fishing for either or both species may be calculated using $(r_i - c_i)$ for (r_i) in equations (5).[3] Equilibrium yield (Y) is given by $c_i L_i'$, where L_i' is the equilibrium value associated with c_i, thus

$$\left.\begin{aligned} Y_1 = c_1 L_1' &= \frac{c_1 [a_2 (r_1 - c_1) - b_1 (r_2 - c_2)]}{a_1 a_2 + b_1 b_2} \\ Y_2 = c_2 L_2' &= \frac{c_2 [a_1 (r_2 - c_2) + b_2 (r_1 - c_1)]}{a_1 a_2 + b_1 b_2} \end{aligned}\right\} \qquad (7)$$

Yield curves for prey and predator at various rates of harvesting follow the familiar dome-shaped pattern (Fig. 1, 2). Increased rates of harvesting

[3]Note that for the predator $(r_2 - c_2)$ may be negative. The rate of reproduction of the predator is augmented by the presence of the prey $(b_2 N_1)$ so that the upper limit to a sustainable rate of exploitation of the predator is given by $c_2 = r_2 + b_2 N_1$.

predators are associated with increases in the yield from the prey population at various rates of fishing. Decreased yields of predators are associated with increases in the rates of harvesting of prey. The fishing intensities associated with the maximum sustained yield for a given rate of fishing on the other species, are in each case given by

$$\left.\begin{aligned} c_1 &= \frac{a_2 r_1 - b_1(r_2 - c_2)}{2a_2} \\ c_2 &= \frac{a_1 r_2 + b_2 (r_1 - c_1)}{2a_1} \end{aligned}\right\} \qquad (8)$$

which are obtained by setting equal to zero the derivatives of equations (7).

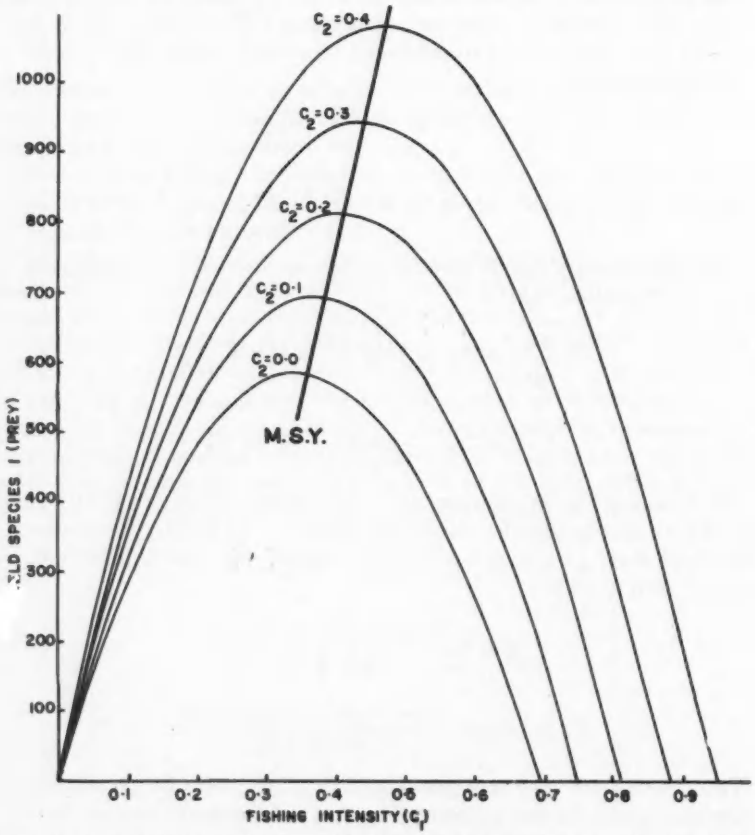

FIG. 1. Sustainable yield of species 1 (prey) in relation to fishing intensity at various levels of fishing species 2 (predator). Values of parameters: $r_1 = 1.0$, $a_1 = .000125$, $b_1 = .00025$, r_2 0.5, $a_2 = .0004$, $b_2 = .000125$. The straight line marked M.S.Y. joins the points of maximum sustained yield at different values of c_2.

Similarly, the expressions giving the fishing intensities associated with a combined maximum sustained yield (the yield of both species combined) may be obtained by partial differentiation of the sum of the right hand sides of equations (7), setting each of the differentials equal to zero and solving simultaneously. The resulting equations in c_1 and c_2 are:

$$\left.\begin{aligned} c_1 &= \frac{2a_1a_2r_1 - a_1r_2\,(b_1+b_2) + b_2r_1\,(b_1-b_2)}{4a_1a_2 - (b_1-b_2)^2} \\ c_2 &= \frac{2a_1a_2r_2 + a_2r_1\,(b_1+b_2) - b_1r_2\,(b_1-b_2)}{4a_1a_2 - (b_1-b_2)^2} \end{aligned}\right\} \qquad (9)$$

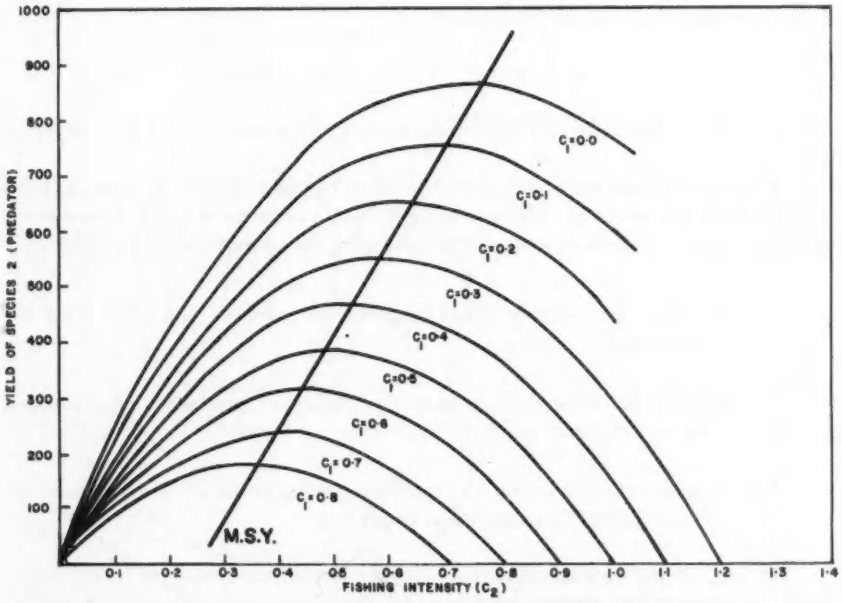

FIG. 2. Sustainable yield of species 2 (predator) in relation to fishing intensity at various levels of fishing species 1. Values of parameters as in Fig. 1. The straight line marked M.S.Y. joins the points of maximum sustained yield at different values of c_1.

These equations must be solved with the restriction that the values of c_1 and c_2 are associated with real positive population sizes. Using the values given in the example of Fig. 1 and 2, the solution of equations (9) is $c_1 = 0.6271$, $c_2 = 1.1695$, but the latter is associated with a negative population of predators and the solution is unreal. In this example the greatest real yield in numbers is associated with elimination of the predators and harvesting prey at $c_1 = 0.5$.

More reasonable is to assume that the two species have different value in which case equations (9) may be modified to represent maximum sustained yield in value. The appropriate expressions are:

$$\left.\begin{aligned} c_1 &= \frac{\lambda\,[2a_1a_2r_1 - a_1r_2\,(b_1+\lambda b_2) + b_2r_1\,(b_1-\lambda b_2)]}{4\lambda a_1a_2 - (b_1-\lambda b_2)^2} \\ c_2 &= \frac{\lambda\,2a_1a_2r_2 + a_2r_1\,(b_1+\lambda b_2) - b_1r_2\,(b_1-\lambda b_2)}{4\lambda a_1a_2 - (b_1-\lambda b_2)^2} \end{aligned}\right\} \qquad (10)$$

where λ is the ratio of the value of an individual of species 2 (predator) to the value of an individual of species 1 (prey).

With λ given a value of 2, the example of Fig. 1 and 2 solves to give maximum sustained value of yield at

$$c_1 = 0.34375 \qquad c_2 = 0.75000.$$

Yield isopleths for various combinations of c_1 and c_2 with $\lambda = 2$ are shown in Fig. 3.

A complete description of the significance to yield of various combinations of values for the seven parameters r_i, a_i, b_i, and λ requires a multi-dimensional representation. In some situations the following ratios may be meaningful:

$\frac{r_1}{r_2}$ indicating the relative potentials for increase of the prey and the predator;

$\frac{b_1}{a_1}$ expressing the effect on the prey population of predation as compared to intraspecific competition;

$\frac{b_2}{a_2}$ expressing the effect on the predator population of prey density as compared to intraspecific competition.

As each of the two latter ratios becomes larger, the intensity of the interaction is greater and the consequences of exploitation of one or both species are magnified. The ratio r_1/r_2, taken in conjunction with λ is instrumental in determining the best relative rates of harvesting the two species.

For study of transition paths and extinction probabilities, a discrete time version of equations (4A) is readily available using the methods developed by Leslie (1958) and Leslie and Gower (1958, 1960).

Using an analogue computer and sacrificing accuracy, the properties of the type of system depicted by equations (4A) may be readily studied, and may be extended to several species, for example a four-species system of two competitors and two predators partially dependent on both prey species, but wholly dependent on neither or both, viz.:

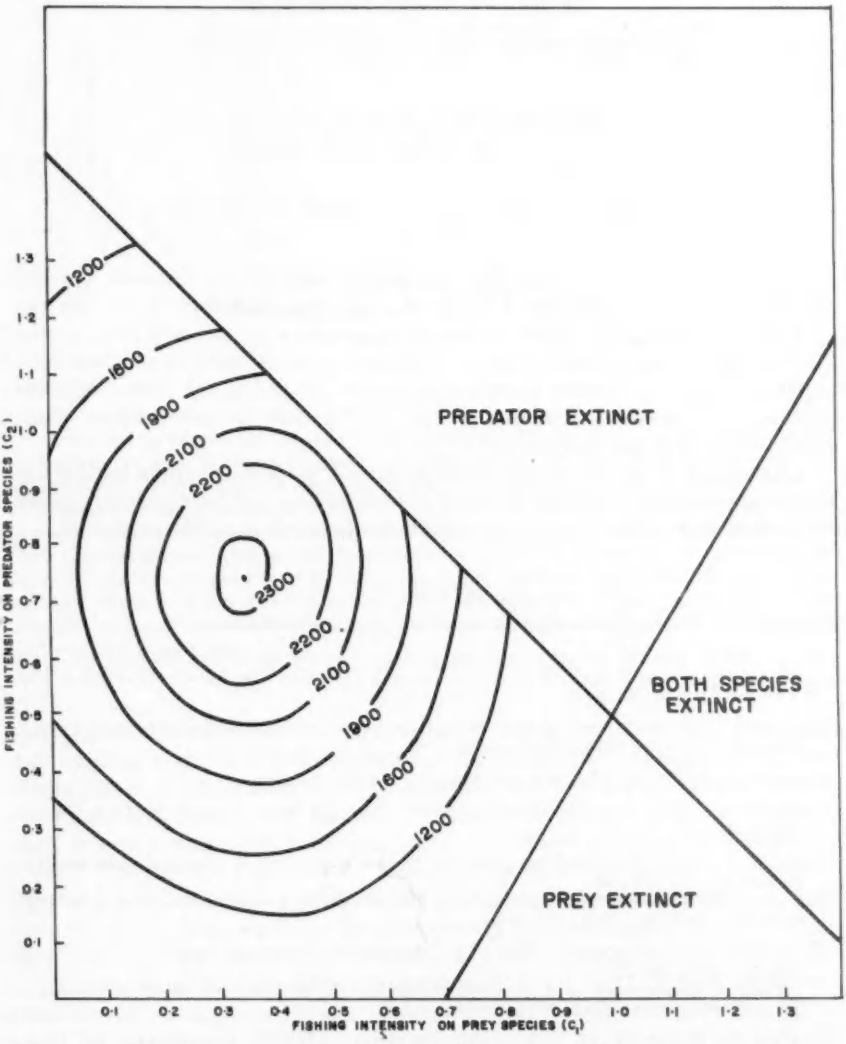

FIG. 3. Isopleths of combined value of yield at different rates of fishing intensity on predators and prey, where the predator is given twice the value of the prey. The values of parameters are as given in Fig. 1 and 2, and with $\lambda = 2$.

$$\left.\begin{aligned}
\frac{dN_1}{dt} &= r_1N_1 - a_1N_1^2 - b_{12}N_1N_2 - b_{13}N_1N_3 - b_{14}N_1N_4 \\
\frac{dN_2}{dt} &= r_2N_2 - a_2N_2^2 - b_{21}N_2N_1 - b_{23}N_2N_3 - b_{24}N_2N_4 \\
\frac{dN_3}{dt} &= r_3N_3 - a_3N_3^2 + b_{31}N_3N_1 + b_{32}N_3N_2 - b_{34}N_3N_4 \\
\frac{dN_4}{dt} &= r_4N_4 - a_4N_4^2 + b_{41}N_4N_1 + b_{42}N_4N_2 - b_{43}N_4N_3
\end{aligned}\right\} \quad (11)$$

where coefficients b_{12} and b_{21} describe competition effects between the prey species; b_{13} and b_{23} indicate the effects of one of the predators on the two prey species; b_{14} and b_{24} the effects of the other predator on the two prey species; b_{31} and b_{32} represent coefficients of increase in abundance of one species of predator related to density of each prey species; b_{41} and b_{42} the same coefficients for the other species of predator; b_{34} and b_{43} describe competition effects between the predator species.

Extended to cover several species, such a system of equations perhaps best represents associatively the type of interlocking but only partially dependent relation which exists between numbers of predators and prey species.

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Occurrence of Dimethyl-β-Propiothetin in Marine Phytoplankton[1]

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ABSTRACT

Dimethyl-β-propiothetin has been reported from several species of freshwater and marine multicellular algae. Cultures of 14 species of unicellular marine algae were treated with cold aqueous alkali. Dimethyl sulphide was liberated from *Syracosphaera carterae, Skeletonema costatum, Amphidinium carteri, Phaeodactylum tricornutum, Tetraselmis* sp. and *Cyclotella cryptica*, and is assumed to arise from dimethyl-β-propiothetin. The amounts of alkali-labile material varied, on a wet weight basis, from 0.07 to 2.9% (as thetin salt) in different organisms. The presence of the thetin in *S. carterae* was confirmed by other means. The thetin, and particularly its degradation products, acrylic acid and dimethyl sulphide, may influence actual fishing operations and also affect the quality of fishery products. The metabolic and ecological significance of these materials are reviewed and discussed.

INTRODUCTION

The presence of dimethyl-β-propiothetin (DMPT) in several species of multicellular algae is well documented (Challenger, 1959; Greene, 1962). The biosynthesis of this thetin from methionine has been demonstrated *in vivo* (Greene, 1962). Its function remains obscure although an "antibiotic" role has been strongly suggested for acrylic acid, a natural degradation product of DMPT (Sieburth, 1960, 1961, 1964a, b; Katayama, 1964a). This acid, together with dimethyl sulfide (DMS), is liberated spontaneously through enzymic action upon death (or merely removal from sea water) of certain algae (Cantoni and Anderson, 1956; Challenger, 1959). If acrylic acid is the more significant material then other suggestions of a role for this acid, in alanine metabolism (Katayama, 1964b), or as a structural element (Sieburth, 1964a) must be considered. DMPT, however, may also be involved structurally (Nicolai and Preston, 1953).

A widespread presence of DMPT in planktonic marine organisms may be inferred from various observations. Motohiro (1962) isolated DMPT from

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North Pacific chum salmon (*Oncorhynchus keta*) and also from the invertebrate *Limacina helicina*. This pteropod forms the principal food of the salmon at the particular time of year when a "petroleum" odour was noted with freshly caught fish. No particular phytoplankter was implicated. The same type of odour, identified as dimethyl sulphide (Sipos and Ackman, 1964), was noted in Labrador cod (*Gadus morhua*) in association with undetermined species of zooplankton. Acrylic acid, presumably associated with DMPT, has been traced by Sieburth (1960, 1961) back from penguin stomachs through the krill (*Euphausia superba*) to a phytoplankter, *Phaeocystis pouchetii*, in Antarctic waters. This same alga is also stated to repel herring in the North Atlantic (Fraser, 1962; Hardy, 1956; Sieburth, 1961). Possibly this is due to a soluble repellent, or merely to the slimy gelatinous masses associated with this organism, although toxicity to young herring has been mentioned with the colonial form of this organism (Parke, *cf.* Sieburth, 1960). The planktonic diatom *Rhizosolenia styliformis* is responsible for a "tobacco juice" odour (Hardy, 1956; Fraser, 1962), and has been related to poor herring fishing but has not been associated, to our knowledge, with DMPT, DMS, or acrylic acid. Similarly, the common planktonic diatom of temperate North Atlantic waters, *Skeletonema costatum*, has been shown to have antimicrobial activity (Sieburth, 1964b; Sieburth and Pratt, 1962; Katayama, 1964a). Finally the identification of DMS as the main volatile flavour component of fresh Pacific oysters (Ronald and Thomson, 1964) suggests that organisms containing modest amounts of DMPT might be ingested by these animals and that DMS is liberated through enzymic breakdown of the DMPT. However, other sources for this DMS cannot be discounted.

To our knowledge no report exists of the occurrence of DMPT in planktonic marine algae. The present survey was initiated to fill this gap since DMPT may have important implications in fishery products (Motohiro, 1962; Sipos and Ackman, 1964). It should be pointed out that the species of marine phytoplankton investigated were grown under artificial conditions and the proportions of DMPT indicated may not reflect accurately those found in the natural state. In addition, the method employed for DMPT estimation is *apparently specific*, but only one of the positive results was further investigated to obtain confirmation of the presence of DMPT by other means.

EXPERIMENTAL PROCEDURES

Culture Conditions

Axenic cultures of unicellular marine algae were grown in SWM-1 medium (McLachlan, 1964), except that the concentration of $NaNO_3$ was increased to 2.0 mM. These organisms were grown at 21 C in Fernbach flasks containing 1 litre of medium. Continuous illumination of approximately 5500 lux was provided by cool-white fluorescent lamps. With the exception of *Syracosphaera carterae*, the flasks were incubated on a rotary shaker. Cultures were normally grown 14 days to harvest. Additional cultures of *S. carterae* were harvested at

intervals up to 14 days and in a further experiment were also grown at a lower light level.

DMPT Estimation

The determination of the DMPT content was based on the presumed specificity of the liberation of DMS from DMPT by cold concentrated alkali (Challenger, 1959; Ackman and Dale, 1965) with gas–liquid chromatographic estimation of the liberated DMS (Ackman and Dale, 1965). Solutions of authentic DMPT chloride were run daily as a quantitative reference and analyses of the cultures (Table II) are reported on the basis of the chloride.

Analyses were carried out on whole cultures (7-ml aliquots), and, after separation by gentle centrifugation, on the supernatant (7-ml aliquots) and on the wet cells (1–5 mg, depending on the concentration of DMPT, with addition of distilled water (7 ml)). Each determination was carried out a minimum of three times and in cases of difficulty (see Discussion) additional analyses were performed.

DMPT Identification

The coccolithophorid, *S. carterae*, was investigated in detail (Tocher, Ackman, and McLachlan, unpublished) and the presence of DMPT confirmed by precipitation as the reineckate with recovery and chromatographic analysis by paper and thin-layer techniques. All steps were monitored by the gas–liquid chromatographic procedure. No precipitable materials giving significant amounts of DMS on treatment with alkali were found excepting that corresponding to DMPT.

EXPERIMENTAL RESULTS

Treatment with cold aqueous alkali solution gave DMS in readily detectable amounts with 6 of the 14 organisms examined (Table I). The sensitivity of the method (Ackman and Dale, 1965) and the use of large samples of wet cells provide good evidence that DMPT was completely absent in the remaining eight organisms. In no instance was free DMS found in significant amounts in whole culture samples.

When DMPT was present the agreement between the whole culture value and other values (wet cells plus supernatant) was satisfactory only in a few instances (Table II). The reproducibility of the whole culture analyses was normally very good except when cell clumping, as in mature cultures of *S. carterae*, introduced some variability in the actual sampling (withdrawal by pipette). Supernatant values were very reproducible. Determination of DMPT on the wet cells was normally more erratic owing to the difficulty in accurately weighing small samples (ca. 1 mg), and also in obtaining such samples homogeneously packed and well drained of medium. *Cyclotella cryptica*, for example, although readily thrown out of the medium, remained as a very fluid mass and could not be as well drained as most of the other organisms. The determination

TABLE I. Unicellular marine algae examined for dimethyl-β-propiothetin (DMPT).

Class and species	DMPT
Chlorophyceae	
Dunaliella tertiolecta	absent
Dunaliella primolecta	absent
Tetraselmis (*Platymonas*) sp.	present
Bacillariophyceae	
Cyclotella cryptica	present
Thalassiosira fluviatilis	absent
Skeletonema costatum	present
Phaeodactylum tricornutum	present
Dinophyceae	
Amphidinium carteri[a]	present
Crysophyceae	
Monochrysis lutheri	absent
Syracosphaera carterae	present
Xanthophyceae	
Olisthodiscus sp.	absent
Bangiophyceae	
Porphyridium sp.	absent
Cryptophyceae	
crytomonad 3-c	absent
flagellate	absent

[a]Isolations from two sources gave similar results.

TABLE II. Estimations of dimethyl-β-propiothetin (as the chloride) based on results of analyses of whole cultures, supernatant, and wet cells.

Organism cultured	Wet cells (*g/litre*)	(DMPT)$^+$Cl$^-$ in mg/litre			Weight % (DMPT)$^+$Cl$^-$
		Whole culture	Supernatant	Wet cells	
Syracosphaera carterae	1.6	21	1	47	2.9[a]
Skeletonema costatum	2.0	7.4	1.6	13.6	0.68[a]
Amphidinium carteri	1.9	13	3	11	0.65[b]
Phaeodactylum tricornutum	~0.7	1.8	~0.05	~2.0[c]	~0.30[b]
Tetraselmis (*Platymonas*) sp.	1.5	2.9	~0.03	1.9	0.19[b]
Cyclotella cryptica	~1.2	0.8	~0.01	>0.4[c]	~0.07[b]

[a]Based on wet cell results.
[b]Based on whole culture results.
[c]Accurate weight not possible due to dilution of wet cells with medium.

of all total wet weights of cells was of course subject to error due to incomplete drainage or small losses of wet cells associated with drainage.

An initial assumption in this study was that the alkali reagent would rapidly penetrate the cells in samples of whole cultures during the standard reaction of 2 min. This was partially justified since in four out of six organisms the whole culture DMPT value was the highest. The wet cells of *S. carterae* from mature cultures packed into a semi-dry mass and did not completely disperse on agitation in distilled water, although in other cases cell lysis was observed. The yields of DMS from the mature cells of *S. carterae* were therefore erratic, but definitely higher than from the whole culture. It is possible that alkali penetration of normal cells is slow and some mechanical rupture assisted in liberating DMPT for reaction in the wet cell determinations. More probably the wet cells may include a high proportion of organized structural elements from ruptured cells, with consequent enrichment in DMPT if this is concentrated as shown for the cell wall of the marine alga *Spongomorpha arcta* (Nicolai and Preston, 1953). Similar reasoning would apply to the *S. costatum* results.

The observation that the DMPT content is proportional to the cell weight and independent of phase of growth in *S. carterae* (Table III) could be interpreted as supporting a structural role for DMPT.

TABLE III. Dimethyl-β-propiothetin (DMPT) content of cultures of *S. carterae* at various growth stages and grown under two different levels of illumination.

Light level and age of culture (*days*)	Wet cell weight (*g/litre*)	$(DMPT)^+Cl^-$ content[a]	
		mg/litre	Weight % $(DMPT)^+Cl^-$ of wet cells
5500 lux			
3	0.3	2.5	0.91
5	0.6	7.0	1.24
7	0.7	8.5	1.19
9	0.9	11.0	1.18
12	1.2	14.4	1.15
14	1.6	16.1	1.01
2000 lux			
3	0.2	2.4	1.37
5	0.5	3.8	0.76
7	0.6	7.3	1.10
9	0.7	8.5	1.10

[a]Based on whole culture result.

It is not clear from the present study whether the DMPT in the supernatant is normally present as an excretory product, is due to lysis of senescent cells, or is released from cells damaged during centrifugation. However, the proportion of DMPT in the supernatant (Table II) was negligible in three cases and modest in the others.

DISCUSSION

The present technique of reaction with cold alkali to yield DMS is believed to be specific for DMPT. Other types of sulfonium compounds may liberate DMS on boiling with alkali (Challenger, 1959; Hino et al., 1962). Some algae evolve DMS only with boiling alkali whereas others evolve DMS with cold alkali (Challenger, 1959). It is reported that *Spongomorpha arcta* evolves DMS with cold alkali and after this reaction has ceased a further evolution may be obtained with hot alkali (Challenger, 1959). This may represent two sulphonium compounds or DMPT may be partially bound in a form resistant to cold alkali (*cf.* Nicolai and Preston, 1953). It is reported (Sieburth, 1964a) that DMS and acrylic acid are found in a high proportion of various species of marine algae examined (mostly multicellular types). It is, therefore, not too surprising that DMPT should be present in a high proportion of planktonic marine organisms as well. On the limited evidence (Table I) there is no reason to consider any one class of organism as particularly associated with DMPT.

Of those organisms containing DMPT, *S. costatum* has been mentioned as having antibiotic properties (Sieburth, 1964b; Sieburth and Pratt, 1962). This alga is at times very abundant in the plankton of North Atlantic waters (Fraser, 1962). The organism containing the highest DMPT level, *S. carterae*, is a coccolithophorid and these forms have been associated with "white waters" favourable to herring catches (Hardy, 1956; Fraser, 1962) although the coccolithophorids concerned are not necessarily of this species.

Hardy (1956) takes the view that the apparent exclusion of herring from certain plankton blooms is due to a "serial" effect, with the lag between phytoplankton and zooplankton population explosions accounting for the absence of herring during phytoplankton blooms. Herring are active but discriminating feeders and migrate according to the availability of zooplankton. Against the report of toxicity of the phytoplankter *P. pouchetii* (colonial form) to young herring (Parke, *cf.* Sieburth, 1960) must be set the fact that oysters have been successfully grown on cultures of *S. costatum* (Landau, 1963). Preliminary experiments (Ackman et al., 1966) have shown that DMPT fed to cod appears harmless and is only partially absorbed by the fish. It is rapidly excreted when intake ceases. No DMS formation was observed. Motohiro (1962) found appreciable levels of DMPT in both chum salmon and *L. helicina*.

It appears likely that DMPT is harmless to higher organisms such as marine invertebrates and fish, and is possibly metabolically utilized to some extent as a methyl donor (Challenger, 1959; Motohiro, 1962). The acrylic acid noted by Sieburth (1960, 1961, 1964a) and Katayama (1964a) as an antimetabolite has not been shown specifically to be associated with DMPT,

although this is very probable. It does not appear toxic to organisms other than bacteria where the coenzyme-A form has been shown to be involved in metabolic functions (Thijsse, 1964). DMS is probably harmless to all organisms, although possibly acting as a repellent. The characteristic "petroleum" or "decaying seaweed" odour (Hardy, 1956; Motohiro, 1962; Sipos and Ackman, 1964) is aesthetically objectionable in raw fishery products (excepting oysters) if originating through natural enzymatic breakdown of DMPT in dead phytoplankton after ingestion by zooplankton, or in canned products where the degradation of DMPT is a thermal process (Motohiro, 1962). The periodic appearance of DMPT and its degradation products in various areas of the world's oceans must correspond to blooms of particular phytoplankton species, but it is probable that most of the time there are present one or more species containing DMPT. Primary plankton consumers such as zooplankton, oysters, etc., may therefore be expected to show trace amounts of DMPT, DMS, or acrylic acid when feeding on a random mixture of phytoplankton. When a bloom in which no DMPT was formed is the predominant food, this level would drop correspondingly.

The biological significance of DMPT remains obscure. However, since it appears to occur widely and presumably in association with acrylic acid it is probable that one or both of these compounds may fall into the category of "secondary" metabolites, analogous to some antibiotics from microorganisms (Brian, 1957) and to many other unusual materials from natural sources (Vining, 1965). These "secondary" metabolites frequently appear in significant quantities only in response to deficiencies in one or more essential nutrients, suggesting that their function is to discourage other types of organisms competing for the same food supply.

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Variability in Life History Characteristics of Steelhead Trout (*Salmo gairdneri*) Along the Pacific Coast of North America[1]

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ABSTRACT

Steelhead enter spawning streams in the lower mainland of British Columbia throughout all months. Those ascending streams between November 1 and April 30 are termed "winter steelhead," while "summer steelhead" enter streams between May 1 and September 30. Cheakamus River is exceptional in that initial stream entry of winter steelhead is delayed until April 1, with most fish entering during April and May. Late entry is related to delayed freshet conditions within this stream. Almost twice as many female as male steelhead were angled. Comparison with trapping results suggests that sport fisheries select for females of anadromous rainbow trout populations. Repeat spawning of winter steelhead was found to range from 5.0% for fish from the Seymour River to 31.3% for Cheakamus River. Repeat spawning among summer steelhead ranged from 4.4% (Seymour River) to 6.3% (Coquihalla River). Mean fork lengths of populations of winter and summer steelhead showed little variation (range 26.3–31.0 inches). Winter steelhead from the Cheakamus River were larger than fish from all other populations while summer steelhead from the Coquihalla River had the least mean length. In general, mean fork lengths of winter and summer steelhead were not greatly different, despite the 5–8-month shorter term of saltwater residence of the latter. However, variations in mean lengths of steelhead between different river systems may result from differences in duration of saltwater residence since mean lengths of these populations did increase with longer saltwater residence. Steelhead spent from 1 to 4 years in fresh water and from 1 to 4 years in salt water.

Along the Pacific coast from central California to southern British Columbia, timing of initial stream entry showed little variation. Sex ratios were nearly 1:1. Incidence of repeat spawning decreased from south to north. Mean fork lengths of steelhead populations were greater in northern areas where fish spent more years in fresh and more years in salt water.

INTRODUCTION

The steelhead trout, *Salmo gairdneri*, distributed along the Pacific coast from California to Alaska, is a highly valued sport fish and contributes substantially to commercial fisheries. In comparison to the extensive studies conducted on other commercially valuable salmonid species and important sport fish species, there have been few extensive studies on the life history and habits of steelhead.

Several investigations have shown that the life histories of steelhead are highly variable (Shapovalov and Taft, 1954; Chapman, 1958; Bali, MS, 1958; Pautzke and Meigs, 1940; Maher, MS, 1954). Furthermore, Bali (MS, 1958)

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has suggested that characteristics of steelhead populations in Oregon streams may change in relation to their geographic distribution. The objectives of the present study are twofold. First, an attempt has been made to compare the characteristics of adult steelhead trout populations of several streams in southwestern British Columbia, and to determine what relationships may exist between these characteristics and their particular stream environment. Second, data relating to steelhead populations along the Pacific coast have been compared to examine the variation which exists between widely separated populations.

MATERIALS AND METHODS

Steelhead populations within southern British Columbia were selected for study where 100 or more scale samples were available from an individual stream. The populations of seven streams were selected on this basis. Also, data for populations of the Chilliwack River tabulated by Maher (MS, 1954) were considered.

The 1374 adult steelhead scale samples used were obtained entirely through a system of voluntary submission by anglers from 1949 to 1958. In this sampling program, anglers were supplied with envelopes for return of scale samples taken from "just behind the back 'dorsal' fin, high up on the side." Locality and date of capture, length and weight of fish, and remarks were recorded by the angler for each sample. Methods of selection, mounting, and reading of scales were identical to those of Maher (MS, 1954).

The following information was tabulated for each fish: locality of capture, sample number, half-month of capture, year of capture, summer or winter steelhead, length, weight, sex, years spent in fresh water, years spent in salt water, number and years of previous spawnings, year of hatching.

Steelhead which enter and ascend streams between November 1 and April 30 are classed as winter steelhead. However, in a few instances, winter fish have been reported captured as early as mid October and as late as May; and in Cheakamus River, all winter fish were captured in April and May. All winter-run fish have well-developed sexual products in preparation for spawning which usually takes place in March and April. Steelhead which enter and ascend streams during May, June, July, and August are named summer steelhead. Summer-run fish have only slightly developed gonads at the time of their entry to streams, as spawning does not take place until early the following spring.

The term "age group" is used to denote the particular combination of freshwater and saltwater life to which a fish belongs. In tables and in the text, winter steelhead age groups are referred to as 2/3, 4/1, etc., the first number representing the time spent in fresh water in years, and the latter number the time spent in the ocean in years. Life-history categories of summer steelhead have been recorded similarly, although in each instance their ocean life is 6 or 8 months shorter than designated as years by the number following the oblique stroke.

Because of the lack of information on summer steelhead from streams other than in southern British Columbia, only winter steelhead are considered

in the section of this work describing characteristics of populations from a wide geographic range.

In a study of steelhead anglers' samples some bias may result from (1) a tendency for anglers to report only larger fish, (2) selectivity for size because of the types of gear used (Larkin, MS, 1949), (3) escape of large fish because of the difficulties of fishing, (4) selection of females by gear, or (5) release of males as inferior fish in the later part of the season.

STEELHEAD POPULATIONS IN SOUTH COASTAL BRITISH COLUMBIA STREAMS

Streams

The eight study streams are situated in the extreme southwest coast of British Columbia (Fig. 1). They drain, either directly or via the Fraser River, to the Pacific Ocean. Five of these rivers drain to the Fraser River 23–100 miles upstream of its mouth; these are, in increasing distance, the Coquitlam, Alouette, Chehalis, Chilliwack, and Coquihalla Rivers. The three remaining streams emptying directly to the Pacific near to Vancouver are the Cheakamus, Capilano, and Seymour Rivers.

A complete year of discharge records for each of the study streams for which this information is available is shown in Fig. 2.

With the exception of Cheakamus River, flow characteristics are fairly similar. Typically, in British Columbia coastal streams, water flows are extremely low during the midsummer months owing to low precipitation and again in midwinter months because of freezing conditions in the upper watersheds. Peak water flows occur in April, May, and June when precipitation is high and ice and snow in headwater areas is melting. A lesser peak usually occurs in October and November when precipitation is again high.

The Cheakamus River is exceptional in that highest water-flows occur from June to September, the normal period of lowest water flows for other coastal rivers. This anomalous situation results from midsummer melting of glaciers feeding some tributary streams of the Cheakamus River.

A complete year of water temperature records for each of the study streams for which this information is available is shown in Fig. 3.

In all rivers water temperatures are low (monthly means of 42 F or less) during the months of December, January, and February. Mean temperatures begin to rise in March with a gradual increase until mid August when mean temperatures range between 50 and 62 F. Water temperatures decrease during the fall and early winter months until midwinter when means between 33 and 42 F are experienced.

All study streams have relatively short water courses with steep gradients (see Table I, Fig. 4). However, reduced gradients and more meandering water courses are found in the lower reaches of the three rivers which flow through the Fraser River delta; these are the Coquitlam, Alouette, and Chilliwack Rivers. Typically, stream beds are composed largely of boulders and gravel,

FIG. 1. Location of the British Columbia study streams.

with little exposed bedrock, sand, or mud. All rivers except the Capilano and Seymour have tributary streams which serve as spawning areas for steelhead.

The Coquihalla River has a waterfall barrier, impassable for winter-run steelhead, 6 miles upstream of the mouth of the river. Consequently, the spawning and rearing area for these fish is restricted to the lower 6 miles of stream. Summer-run steelhead can pass this obstruction; they spawn within the 18 miles of river above the obstruction. A similar, but more easily passable barrier existed in Capilano River 3 miles upstream of the river mouth until 1954 when a domestic water storage reservoir was constructed in this area.

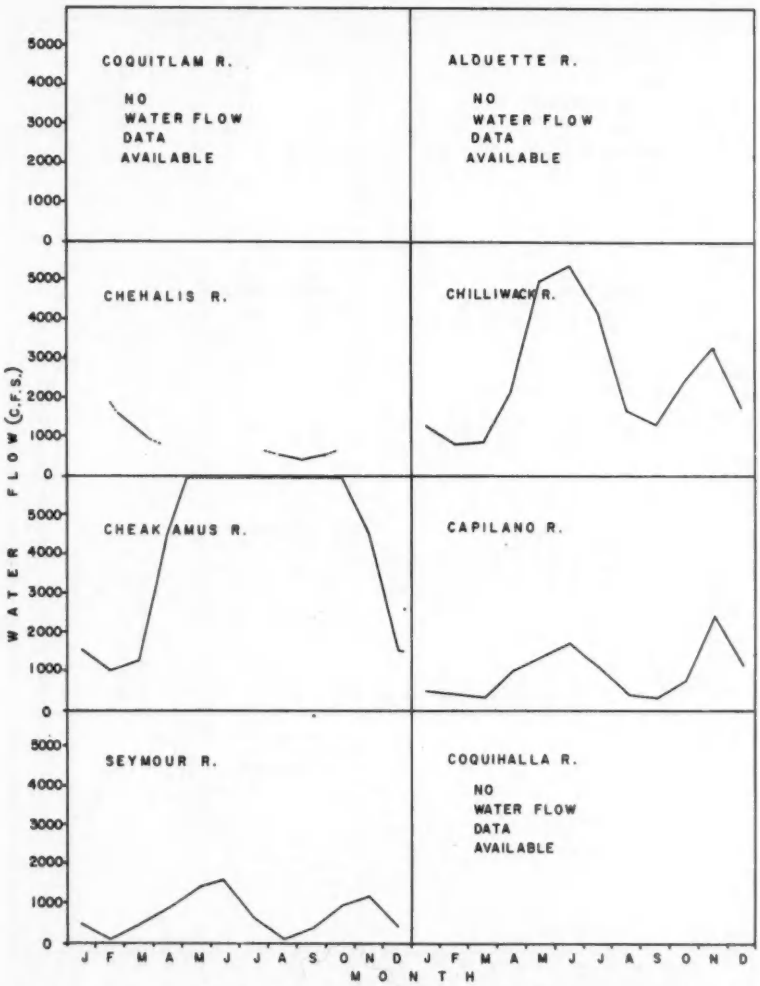

FIG. 2. Mean monthly discharge for all streams for which data are available. Flow data for the Chehalis River were obtained during 1956, for the Chilliwack, Cheakamus, and Seymour Rivers from October 1955 to September 1956, and for the Capilano River from October 1954 to September 1955.

STEELHEAD POPULATIONS

TIMING OF STREAM ENTRY

Figures 5 and 6 indicate that there is a marked variation in timing of entry of greatest numbers of adult steelhead into the streams studied.

The greatest number of steelhead were captured during January, with decreasing numbers captured in February and least numbers in March. In

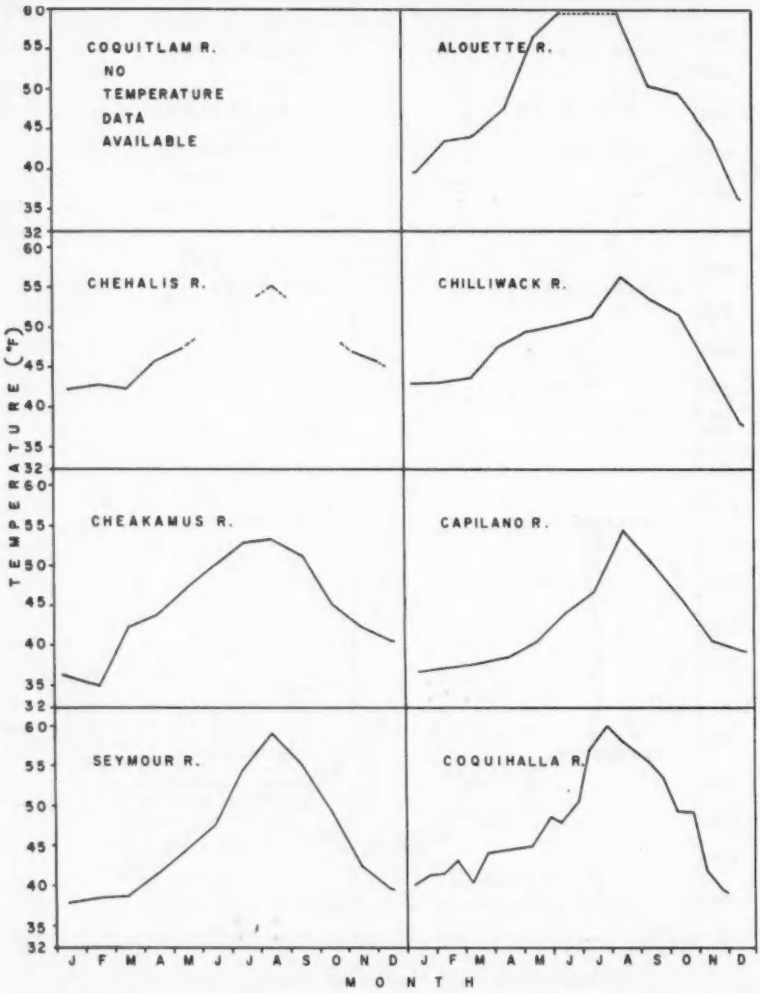

FIG. 3. Mean monthly water temperatures for all streams for which data are available. Temperature data for Chehalis, Chilliwack, and Cheakamus Rivers were obtained during the period January to December 1958, for Capilano River during 1951, for Alouette River during September 1960 to August 1961, and for Coquihalla River from January to August 1958 and September to December 1959. Data for the Seymour River represent mean temperatures from 9 years of recording, 1951–59.

Capilano and Seymour Rivers, however, greater numbers of fish were captured during both February and March than during January. In Cheakamus River all fish were captured during April and May. Appreciable numbers of steelhead were captured from the Capilano, Alouette, Coquitlam, and Chehalis Rivers

TABLE I. Physical characteristics of the British Columbia study streams.

River	Length (*miles*)	Drainage area (*sq miles*)	Gradient[d] rise (*ft/mile*)	Water flow (*cfs*) mean monthly		Water temp (*F*) mean monthly		Lake present in drainage	
				Minimum	Maximum	Minimum	Maximum	Elevation (*ft*)	Area (*acres*)
Coquitlam	37	77	68	–[b]	–[b]	–[b]	–[b]	350	6000
Alouette	27	79	34	–[b]	–[b]	36.6 Dec.	61.6 June	384	3994
Chehalis	20	148	50	–[b]	–[b]	–[b]	–[b]	750	2500
Chilliwack	50	450	57	817 Feb.	5,350 June	34.0 Feb.	53.8 Aug.	2,052	2957
Cheakamus	35	765	25	1,030 Feb.	18,200 July	33.3 Feb.	51.1 Aug.	–[a]	–[a]
Capilano	22	68	66[c]	377 Mar.	2,370 Nov.	34.4 Jan.	52.0 Aug.	–[a]	–[a]
Seymour	28	68	60[c]	78 Aug.	1,560 June	35.5 Jan.	58.0 Aug.	650	250
Coquihalla	40	360	65[c]	–[b]	–[b]	38.1 Jan.	56.2 Aug.	3,750	400

[a]Reservoir established since conclusion of study period.
[b]No information available.
[c]Seasonal barrier in stream.
[d]Gradient of stream to upper limit of steelhead ascent.

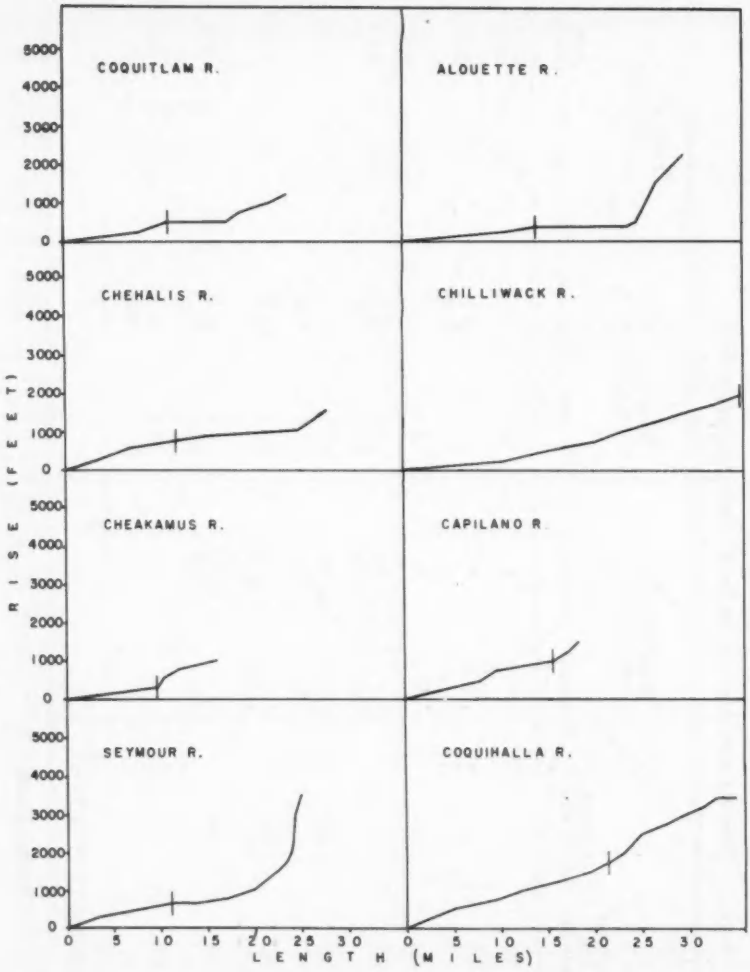

FIG. 4. Profiles of the study streams. Broken line represents upper limit of stream frequented by steelhead.

during December. Angling return information probably gives a fairly accurate index of the proportion of steelhead entering streams in various months.

All winter-run fish have well-developed gonads in preparation for spawning which takes place in March and April. Winter steelhead were captured in each of the study streams.

The Capilano, Seymour, and Coquihalla Rivers contained summer steelhead. Figure 6 shows the duration of the capture period and number of fish taken within these streams. Timing of adult steelhead entry to the Capilano

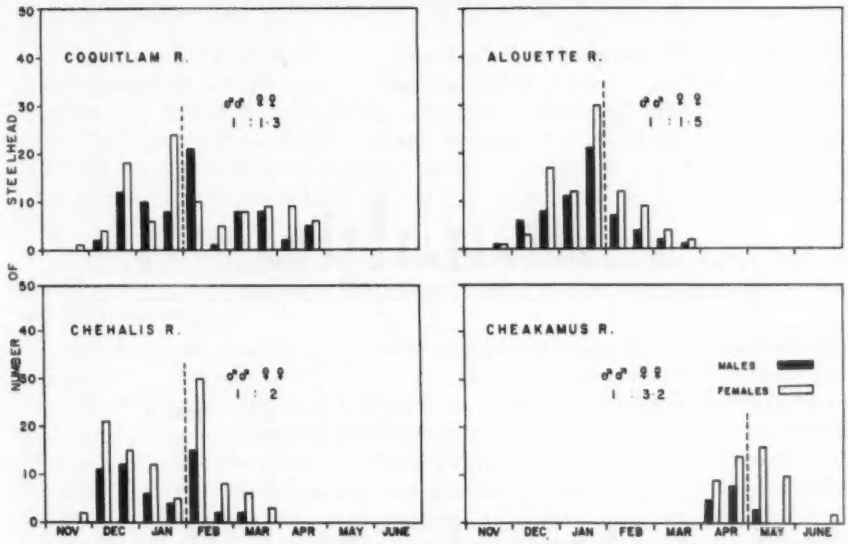

FIG. 5. Number of steelhead captured in half-monthly intervals from streams maintaining winter-run steelhead only (broken line represents division to early and late portions of winter run of steelhead). Ratios represent total numbers of male: female steelhead captured.

and Seymour Rivers is similar; but summer steelhead enter Coquihalla River later in the year. During April, steelhead entering the Capilano River trapping facilities are of two groups, distinguished by their degree of gonad development. Approximately one-half of the fish have well-developed gonads in preparation for spawning which follows shortly; the remainder have only slightly-developed gonads for spawning the following spring. The former group may be classified as "winter" steelhead which are late to enter the river; the latter are "summer" steelhead. Probably fish entering the Seymour River during April are in similar stages of development.

Summer-run fish have only slightly-developed gonads at the time of their entry to streams as spawning does not take place until early the following spring. Summer steelhead were captured in three of the eight streams studied. These streams are not closely related geographically. Two of the rivers supporting runs of summer steelhead (Capilano and Seymour Rivers) drain directly to the ocean via Burrard Inlet, while the Coquihalla River drains to the Fraser River 100 miles upstream of its mouth.

The three streams which maintain groups of both summer and winter steelhead support a fishery throughout almost all months of the year. Winter steelhead first enter these streams during December and fish continue to enter and ascend streams until April and May. During these latter months early summer-run fish are captured in small numbers. In the Coquihalla River a few summer steelhead are captured immediately prior to the arrival of the first

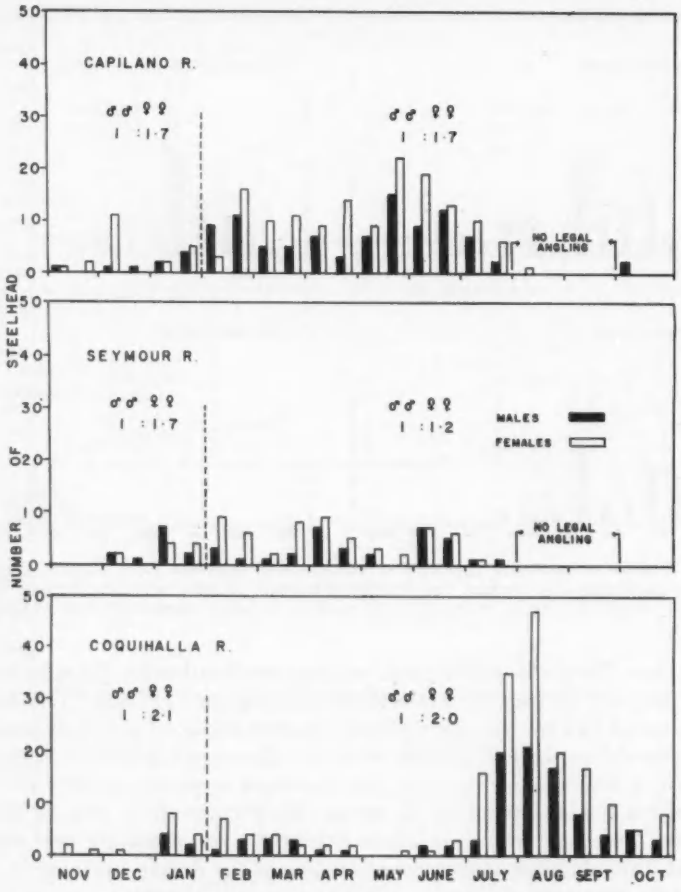

FIG. 6. Numbers of steelhead captured in half-monthly intervals from streams maintaining summer and winter runs (broken line represents division to early and late portions of winter run of steelhead). Ratios represent numbers of male: female steelhead captured during winter and summer runs.

winter-run fish. A somewhat similar situation exists in the Capilano and Seymour Rivers.

The existence of populations of "winter" and "summer" runs throughout most of their range is a unique feature of steelhead populations, although district "spring" and "fall" runs of Atlantic salmon in eastern Canada have been reported by various authors (Belding and Kitson, 1934; Huntsman, 1939). This is a phenomenon not readily observed in Pacific salmon populations except for chinook salmon of the Columbia River system which migrate in three classes and the fish are referred to as spring-run, summer-run, and fall-run chinooks (Burner, 1951).

SEX RATIOS

Figures 5 and 6 show the sex ratio of adult steelhead captured within the study streams in 2-week intervals for the period of record. A striking feature of these data is that females almost invariably outnumber males in each half-month interval of the capture periods. Females comprised between 56.5 and 76.1% of the total captures of winter steelhead from each stream. The greatest difference in ratio of males to females, 1:3.2, occurred in the Cheakamus River (Fig. 5).

Number of males exceeded females captured during only one period in the Alouette and Coquihalla Rivers, and twice in the Coquitlam, Capilano, and Seymour Rivers.

The captures of adult winter steelhead for each of the study streams were arbitrarily divided into "early" and "late" stream entrants by grouping captures from November 1 to January 30 as early entrants, and captures from February 1 to April 30 as late entrants (divided by dotted line in Fig. 5 and 6). In the Cheakamus River the month of April served as the early part of the season; the month of May served as the late portion. Percentages of males captured in the early and late portions of the capture period were compared for each stream (Fig. 5 and 6). Greater percentages of males were captured in the early portion of the capture period in the Alouette, Chehalis, Cheakamus, and Seymour Rivers, and in the late portion in the Coquitlam, Capilano, and Coquihalla Rivers. No trend toward early or late entry of males or females was evident from this analysis.

Ratios of males to females captured in summer fall within the range of the sex ratios for captures of winter steelhead in all study streams (Fig. 6).

Although these data show that many more female than male steelhead of both winter and summer runs are captured by anglers, trapping studies on other Pacific coastal streams strongly indicate that females are present in equal, or near equal, numbers to males (Shapovalov and Taft, 1954; Pautzke and Meigs, 1940; Chapman, 1958).

REPEAT SPAWNING

Of 618 winter steelhead examined, 54 or 8.7%, were returning to spawn for the second time and 11 or 1.8% for the third time (Table II). Second spawners were recorded from all the streams. Winter-run steelhead returning to spawn for the third time were recorded from only four (Alouette, Coquitlam, Cheakamus, and Coquihalla Rivers) of the seven study streams. No fish were recorded returning to spawn for a fourth time. The greatest percentage of repeat spawners was recorded from the Cheakamus River; 31.3% of all winter steelhead captured during 1954, 1955, and 1957, the years of available record, were returning to spawn for a second or third time.

Table II shows that female repeat spawners predominate among the captures. In each stream except the Seymour and Coquihalla Rivers, where only two repeat spawners were captured, more second spawning females than

TABLE II. Numbers of repeat-spawning winter steelhead captured from British Columbia streams for all years of record, 1949–58.

River	Number of fish in sample	Number of repeat spawners	Percentage repeat spawners	Second spawners				Third spawners				Ratio male:female
				Male		Female		Male		Female		
				No.	%	No.	%	No.	%	No.	%	
Alouette	132	19	14.4	3	2.3	12	9.1	2	1.5	2	1.5	1:2.6
Coquitlam	148	8	5.4	1	0.7	4	2.7	0	0	3	2.0	1:7
Chehalis	125	8	6.4	1	2.6	7	8.1	0	0	0	0	1:7
Chilliwack[a]	754	44	5.8									1:8
Cheakamus	64	20	31.3	1	1.6	16	25.0	1	1.6	2	3.1	1:9
Capilano	77	6	7.8	2	2.6	4	5.2	0	0	0	0	1:2
Seymour	41	2	5.0	1	2.5	1	2.5	0	0	0	0	1:1
Coquihalla	31	2	6.4	0	0	1	3.2	0	0	1	3.2	–

[a]Data from Maher (1954).

males were captured. Considering both second and third spawners, females represent 81.5% of all repeat spawners captured.

Of 302 summer steelhead examined, 15 or 5.0% were returning to spawn for the second time and 1 or 0.3% for the third time (Table III). Repeat spawning was observed in 4–7% of the captures from populations of summer steelhead.

As was found for winter steelhead, numbers of female repeat spawners greatly exceeded males. Eighty-nine per cent of the repeat spawners were females.

LENGTHS OF ADULT STEELHEAD

The mean fork lengths of male and female summer- and winter-run steelhead captured within the study streams are shown (for bimonthly intervals) in Appendix 1.

The mean length of winter steelhead was 28.4 inches for males and 28.2 inches for females. Within each stream, males were of greater mean length than females except in the Coquitlam and Chehalis Rivers (Table IV). Comparing lengths of samples from all study streams from which winter-run fish were captured, both males and females from the Cheakamus River had the greatest mean length, 31.0 and 30.2 inches, respectively. Males with the least mean fork length (26.6 inches) were captured from the Coquitlam River, while females with the least mean length (26.9 inches) were captured from the Alouette River. Maher (MS, 1954), for the Chilliwack River, concluded that "... in nearly all cases the mean male length and weight was slightly higher than that of the female..."

Mean length of male summer steelhead was 28.2 inches, and of females was 26.9 inches. Within each study stream males were of greater mean length than females. Males from the Seymour River had the greatest mean length (30.3 inches), while females from the Capilano River had the greatest mean length (28.0 inches). Males (27.3 inches) and females (26.3 inches) with the least mean length were captured from the Coquihalla River.

Appendix 1 indicates that considerable variability exists in mean length of summer steelhead captured in each bimonthly period.

The mean length of male winter steelhead was 28.4 inches; male summer steelhead had a mean length of 28.2 inches. Female winter steelhead had an average length of 28.2 inches, while female summer steelhead had a mean length of 26.9 inches. These lengths are surprisingly similar considering that summer steelhead ascend streams 5–8 months preceding the normal 1–4 complete years of ocean residence experienced by winter steelhead. Stomach samples of summer steelhead from Coquihalla River were largely empty suggesting that little feeding occurs in fresh water (S. B. Smith, personal communication). Presumably growth in length ceases under these circumstances. Belding and Kitson (1934) found that a similar condition prevails with early-run and late-run Atlantic salmon. Measurements of salmon entering the Miramichi River showed practically no difference in length between early- and late-run fish, in spite of the

TABLE III. Numbers of repeat-spawning summer steelhead captured from British Columbia streams for all years of record, 1949–58.

River	Number of fish in sample	Number of repeat spawners	Percentage repeat spawners	Second spawners				Third spawners				Ratio male:female
				Male		Female		Male		Female		
				No.	%	No.	%	No.	%	No.	%	
Capilano	99	6	6.1	0	0	6	6.6	0	0	0	0	–
Seymour	45	2	4.4	0	0	2	4.4	0	0	0	0	–
Coquihalla	158	10	6.3	2	1.3	7	4.4	0	0	1	0.6	1:4

TABLE IV. Mean fork lengths (inches) of winter and summer steelhead for all years of record, 1949–58.

River	Mean fork length of winter steelhead		Mean fork length of summer steelhead	
	Male	Female	Male	Female
Alouette	28.4	26.9		
Coquitlam	26.6	27.2		
Chehalis	29.3	29.5		
Cheakamus	31.0	30.2		
Capilano	28.8	28.1	29.2	28.0
Seymour	29.3	28.9	30.3	27.5
Coquihalla	28.7	27.0	27.3	26.3

longer sojourn and longer feeding period of the latter in salt water, indicating that the larger or more advanced salmon tended to enter the river earlier. Conversely, growth of winter steelhead may cease in the last few months of ocean residence as gonad development commences.

LIFE-HISTORY CATEGORIES

Table V shows the life-history categories of winter steelhead from each of the study streams. Fourteen different life-history categories are represented.

Steelhead which had spent 2 or 3 years in fresh water (i.e., 2/, 3/) before migrating to the ocean and which had spent either 2 or 3 years in salt water (i.e., /2, /3), comprised 91.6% of the total sample from all streams. Yearling smolts (1/) were found only in the Alouette River, where they represented only 8.4% of the samples. Steelhead which had migrated to the ocean as smolts at the age of 2 or 3 years were found from all streams and were 39.9 and 54.9%, respectively, of total samples from all study streams. Only in samples from the Alouette River (and from the Chilliwack River from data of Maher (MS, 1954)) were 2-year-old migrants more numerous than 3-year-old migrants. Four-year-old migrants were also captured from all study streams, but were only 3.4% of all samples.

All winter steelhead captured had remained in salt water for a period of 1–4 years following migration from fresh water and prior to returning to fresh water to spawn. Individuals which had spent 1 year in salt water were uncommon (1.1% of the total sample). Steelhead which had spent 4 years in salt water comprised 2.6% of the total sample. Two- and three-year saltwater resident fish were 96.3% of the total sample.

The youngest winter steelhead captured were of the 1/2 age group; three of these were captured from the Alouette River. The oldest individuals captured

TABLE V. Life-history categories of winter and summer steelhead captured from the British Columbia study streams for all years of record, 1949–58.

	Alouette	Coquitlam	Chehalis	Cheakamus	Chilliwack[a]	Capilano[b]	Seymour[b]	Coquihalla[b]	Capilano[c]	Seymour[c]	Coquihalla[c]
1/1					1 0.1%						
1/2	3 2.3%				8 1.0%				1 1.3%		1 0.7%
1/3	6 4.6%				6 0.8%						
1/4	2 1.5%										
2/1		1 0.7%			2 0.2%		1 1.7%	2 5.1%			3 2.0%
2/2	42 32.1%	34 23.3%	9 8.2%	10 15.6%	239 31.0%	18 25.7%	11 18.9%	6 15.4%	5 5.7%	4 16.0%	23 15.3%
2/3	42 32.1%	14 9.6%	12 10.8%	16 25.0%	236 30.6%	14 20.0%	7 12.1%	3 7.7%	9 10.3%	6 24.0%	1 0.7%
2/4	2 1.5%			3 4.7%	1 0.1%						
3/1					1 0.1%		2 3.4%		1 1.2%		12 8.0%
3/2	21 16.0%	72 49.3%	37 33.3%	22 34.4%	136 17.9%	28 40.0%	22 37.9%	19 48.8%	42 48.3%	12 48.0%	94 62.6%
3/3	11 8.3%	20 13.7%	38 34.2%	10 15.6%	133 17.3%	9 12.9%	13 22.4%	7 17.9%	27 32.0%	3 12.0%	7 4.7%
3/4	1 0.8%	4 2.7%	1 0.9%	2 3.2%	3 0.4%		1 1.8%		1 1.2%		
4/1							1 1.8%				3 2.0%
4/2		1 0.7%	9 8.1%	1 1.6%	1 0.1%	1 1.4%					6 4.0%
4/3	1 0.8%		5 4.5%		3 0.4%			2 5.1%			
4/4											
Totals:	131	146	111	64	770	70	58	39	86	25	150

[a]Data from Maher (1954)
[b]Winter steelhead.
[c]Summer steelhead.

were a total of eight steelhead from the Alouette, Chehalis, and Coquihalla Rivers with a life-history category of 4/3, and a total of eight steelhead from the Alouette, Coquitlam, Chehalis, Cheakamus, and Seymour Rivers with a life-history category of 3/4.

In these data, no trend toward early or late entry of particular age groups was found. Shapovalov and Taft (1954) found that representation of various age groups of winter-run steelhead within the run to Waddell Creek, California, is not the same throughout the season. The /1 fish of smaller size predominated in the early part (November, December, January) of the run; the /2 fish appeared in increasing numbers as the season progressed (February, March); and the larger /1 fish increased in abundance during the late portion of the run (March, April). Similar phenomena have not been reported by other investigators.

Ten different age classes are represented in Table V. Considerable variation exists in the percentages of each life-history pattern represented from stream to stream (Table V). However, in all streams there are some similarities among life-history categories. For example, in most streams 3-year-old migrants outnumber 2-year-old migrants and adult steelhead representing the life history category 3/2 were captured in greater numbers than were those of a 3/3 pattern.

There are large differences in the ratio of fish which had spent 2 years in salt water to those which had spent 3 years in this environment. In the Capilano River the ratio of /3 to /2 fish captured is 1:1.3, in the Seymour River 1:1.8, and in the Coquihalla River the ratio is 1:15.5. Also, a much higher percentage of fish which had spent only 1 year in salt water were captured from Coquihalla River than from other streams. No trend toward early or late season entry to streams of summer steelhead of particular age groups was evident.

Length at maturity is related to the length of saltwater residence of steelhead. Maher (MS, 1954) has shown that winter steelhead from the Chilliwack River attain a length of approximately 19 inches after 1 year of saltwater life, 28 inches after 2 years, and 32 inches after 3 years. The shorter average term of saltwater residence experienced by summer steelhead of the Coquihalla River is reflected in the smaller mean size at capture for these fish noted in the discussion of adult lengths. At capture, summer steelhead from the Capilano and Seymour Rivers were of 1.8 and 1.9 inches greater mean length than were those from the Coquihalla River.

STEELHEAD POPULATIONS OF THE PACIFIC COAST

In the following section life-history characteristics of steelhead populations from a wide geographical range (central California to southern British Columbia) are compared.

Streams

The location of the streams considered in this section is shown in Fig. 7. Some physical features of each stream are given in Table VI, and water temperatures, expressed as a mean of daily recordings at monthly intervals, are shown

FIG. 7. Location of the Pacific coast study streams.

in Fig. 8. Temperature data for the Capilano River are included for comparison with more southerly streams. No temperature data are available for Green River, Washington; however, water temperature data for the Chehalis River (in central coastal Washington) are presented in Fig. 8, assuming that these data are generally representative of temperatures experienced in most larger streams containing steelhead in Washington.

No discharge data are presented, but water-flow patterns are similar in all streams in that heaviest precipitation and greatest flows are experienced in winter and spring months and low flows prevail during summer and early fall.

All streams arise in the coast range of mountains and are precipitous. The streambeds are composed of boulders and coarse and fine gravel with little

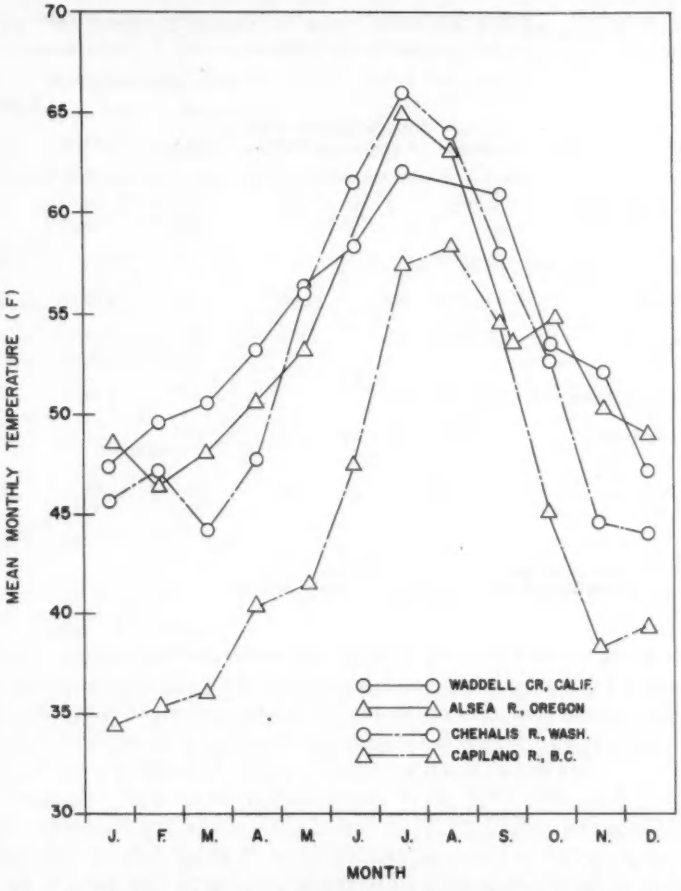

FIG. 8. Mean monthly water temperatures for a complete year of record for some coastal study streams.

sand or mud. Bali (MS, 1958) has compared the physical and biological features of 14 streams of Oregon containing steelhead populations. He has noted that the physical characteristics of the streams are similar, but similarities among life-history characteristics of some geographically related steelhead populations have allowed for grouping of these streams into four south coastal and nine north coastal streams (and one intermediate stream not included in this study).

STEELHEAD POPULATIONS

TIMING OF RUNS

A comparison of data from the study streams shows that in the central and southern parts of their geographic range, winter steelhead first enter and

TABLE VI. Physical characteristics of the Pacific coastal study streams.

	Latitude	Length (*miles*)	Drain. area (*sq miles*)	Water temperature (*F*) Minimum	Maximum	Lake present in drainage
Waddell Creek, Calif.	37°6′N	12	26	36 Jan.	68 Sept.	No
South coastal streams, Ore.	42°30′N	25–113	–[a]	–[a]	>70	No
Coquille River, Ore.	43° 0′N	60	1,060	–[a]	>70	No
Alsea River, Ore.	44°30′N	35	477	41 Feb.	73 July	No
North coastal streams, Ore.	45° 0′N	25–113	–[a]	–[a]	>70	No
Green River, Wash.	47°30′N	86	–[a]	40 Range	55	No
Capilano River, B. C.	49°15′N	22	68	35 Jan.	58 Aug.	No[b]

[a]No information available.
[b]Reservoir established since conclusion of study period.

ascend streams to spawn during a relatively restricted time period (October 15 to November 15). Samples reported throughout the capture period suggest that in south and north coastal streams almost equal numbers of fish enter streams during December and January; the greatest number enter during February and thereafter numbers decrease. However, this study and others (Shapovalov and Taft, 1954; Bali, MS, 1958) have shown that variations in timing of stream entry and seasonal variations in timing of the bulk of the migration do exist. The existence of two peaks of stream entry at Waddell Creek, California, has been shown to be a consequence of migration timing of steelhead of particular age classes. This phenomenon has not been documented elsewhere although observations from the Green River, Washington (Pautzke and Meigs, 1940), suggest that a similar situation obtains there. Unfortunately, the anglers' samples utilized in this present study and those used by Bali in Oregon would tend to mask such an effect.

Spawning occurs in all study streams during April and early May. Capture of spawned fish or "kelts" commences shortly afterward.

SEX RATIO AND REPEAT SPAWNING

Sex ratios of steelhead populations show no regular change from the southern portion of their range to the more northern ones (Table VII). The trapping records of Shapovalov and Taft in California, Chapman (MS, 1957) in Oregon, and Pautzke and Meigs (1940) in Washington show that a male: female sex ratio of near 1:1 is found among adult steelhead populations of

TABLE VII. Sex ratios and frequency of repeat spawning of steelhead captured from Pacific coastal study streams.

	Sex ratio of total run male:female	Repeat spawners	Second spawners	Third spawners	Fourth spawners
		%	%	%	%
Waddell Creek Calif. (T)[a]	1:1.1	17.2	15.0	2.1	0.1
South Coast Ore. (A)	1:1.8	53.3	36.3	14.1	3.0
Coquille River Ore. (A)	1:1.4	38.3	30.9	4.9	2.5
North Coast Ore. (A)	1:1.6	27.9	19.5	6.3	1.9
Green River Wash. (T)	1:1	5.0			
South coast B. C. (A)	1:1.8	11.0 (avg 1949–57)	9.5	1.5	

[a]T = trapped; A = angled.

these geographically separate areas. The greater proportion of females (1 male:1.13 females) in the adult run to Waddell Creek is largely a result of the influence of the disproportionate survival of female repeat spawners over males and a high incidence of repeat spawners in the total run.

A comparison of sex ratios obtained from sampling by trapping and angling may be obtained from Table VII. Angling apparently selects a greater proportion of female steelhead than is representative of the population, and therefore is unreliable as a method of determining the sex ratios of the total population.

At Waddell Creek it was found that males predominated in the spawning run in the early months (November, December), and that females were more numerous in the later portions of the run (January–March). Bali (MS, 1958) has reported similar findings for streams of south and north coastal Oregon. These differences have not been found to exist in other of the study streams.

Within each study stream there is a sharp decline in numbers from second spawners to third spawners and fish spawning for a fourth time represent a negligible portion of the total run (Table VII).

Survival following spawning has been found to be higher among females than among males in all areas (Shapovalov and Taft, 1954; Bali, MS, 1958; Pautzke and Meigs, 1940). Higher survival of females after first spawning explains, in part, the greater numbers of females captured by anglers. Within Oregon, Bali (MS, 1958) has related the greater number of female steelhead

captured in south coastal than in north coastal streams to the higher survival of spawners in southern streams.

Table VII indicates that repeat spawning steelhead are fewer in number in north coastal populations. This trend supports the finding of Bali who has described a similar phenomenon for coastal streams of Oregon. Also, the ability of individual steelhead to return to spawn in successive years appears to decrease in more northern streams. No fourth spawning steelhead were reported from Oregon, Washington, or British Columbia.

LENGTHS AND LIFE-HISTORY CATEGORIES

Shapovalov and Taft (1954) studied lengths of all adult steelhead captured during a 9-year trapping study at Waddell Creek. The mean length of all adult winter steelhead captured in the upstream trap in all years of study was 22.9 inches.

In Oregon the mean length of all steelhead captured from the Alsea River by Chapman in a tagging study extending from 1951 to 1956 was 25.5 inches. Bali, analyzing angler sample data from numerous watersheds of coastal Oregon found that the mean length of fish from the southern region was 26.1 inches, from the central region 26.3 inches, and from the northern region 26.5 inches.

In British Columbia, Maher (MS, 1954), analyzing anglers' samples from the Chilliwack River, found the mean length of all adults captured to be 29.7 inches. The mean length of all fish sampled for the present study was 28.3 inches. If the possible bias of anglers toward retaining and reporting upon larger fish may be disregarded, it is apparent that, generally, the mean size of steelhead entering streams to spawn increases in more northerly areas. This effect is apparent at least from central California to southern British Columbia.

The differences noted in mean lengths of geographically separate steelhead populations can be explained, at least in part, by a tendency for fish from more northern areas to spend a greater length of time in the ocean before sexual maturity is attained. Table VIII illustrates this trend. Steelhead which have spent only 1 year in salt water decline from 46.5% of the total adult population at Waddell Creek, California, to only 0.5% of the adult population in the Chilliwack River, B.C. Numbers of /2 fish remain fairly constant in each area, while a progressively greater number of /3 fish are found in more northern areas. Numbers of /4 fish are fairly constant throughout their range.

The percentage of smolts in each age category (1/, 2/, 3/, 4/) is fairly uniform in each area (Table VIII) except for those from British Columbia streams used in this study. Here, 3-year-old smolts were more abundant than 2-year-old migrants.

DISCUSSION

Steelhead may be divided into two different groups by differences in behaviour prior to spawning and, to a limited extent, by their appearance.

TABLE VIII. Mean lengths and age composition of adult steelhead captured within coastal study streams.

	Mean length of adults (*inches*)	Freshwater residence				Saltwater residence			
		1/	2/	3/	4/	/1	/2	/3	/4
		%	%	%	%	%	%	%	%
Waddell Creek, Calif.	22.9	10.1	72.3	16.7	0.9	46.5	47.0	6.0	0.5
South coastal streams, Ore.	26.1	0.7	43.0	53.3	3.0	85.2	14.1	0.7	–
Central coastal streams, Ore.	26.3	–	54.4	44.4	1.2	50.6	44.4	5.0	–
North coastal streams, Ore.	26.5	6.9	71.7	21.4	–	25.0	64.7	10.3	–
Green River, Wash.	–[a]	16.0	75.0	9.0	–	7.0	66.0	25.0	–
Southern B. C. study streams	28.3	1.8	39.9	54.9	3.4	1.1	59.1	37.2	2.6

[a]Data not available.

Smith (1960) has described differences in physical appearance among spawning summer and winter steelhead from the Capilano River. Summer steelhead exhibited a typical bright red "rainbow" coloration on the gill covers and along the lateral line, and males had well-developed hooked snouts. Both of these characteristics were largely absent among winter fish spawning at the same time. Of greatest interest is the finding by Smith (1960) that among a sample of 30 summer and winter steelhead, all summer fish examined exhibited gill raker tips which were flattened and bifurcated. Winter fish did not exhibit this characteristic. These findings suggest that morphological differences may exist, at least among adult forms, which will distinguish these populations more adequately. Also, artificially spawned juvenile steelhead of "winter" and "summer" stock have been planted in the Capilano River. To date returning adults have been in the same stages of sexual maturity as were their parents at capture. That is, none of the summer steelheads' progeny returned as winter fish, and none of the winter steelheads' progeny returned as summer fish. The populations, for Capilano River at least, appear to be separated by strongly heritable characteristics.

Adult sockeye salmon exhibit "racial" variations in timing of entry to spawning streams. Gilhousen (1960) has concluded that "normal" or mean timing has arisen through evolution by selective processes, the mean value representing the optimum point of survival conditions for a particular race. It is difficult to explain the early migrations of summer steelhead on a basis of selection for optimum stream conditions. During summer and early autumn months stream water levels are low and water temperatures are high, conditions which do not favour survival of salmonids. Belding and Kitson (1934) have postulated that early river entry of some groups of Atlantic salmon

is associated with precocity or accelerated development. Precocious gonadal development apparently is not a prime cause of upstream migration of summer steelhead. Examination of fish sampled at the Capilano River trapping facilities has shown gonads to be but slightly developed.

Within British Columbia, observation of the topography of streams containing populations of summer steelhead suggests that natural temporary barriers (small waterfalls, stretches of extremely turbulent water) which are navigable by fish only at summer water flows may be present within all streams which contain these populations. Partial barriers are present within the Seymour and Coquihalla Rivers, and such a barrier was present in the Capilano River prior to establishment of a reservoir. Barriers of this type may allow upstream passage of only the early, more vigorous stream entrants. This condition would tend to perpetuate an isolated population of separately reproducing, early migrating adult steelhead, the so-called summer steelhead

Instances of delayed entry to streams of winter steelhead similar to that observed for the Cheakamus River have not been reported elsewhere. This late winter run coincides with the delayed freshet condition which exists within the stream (Fig. 2). Correlation of the late run with the increased water volumes suggests that a freshet condition is required to initiate upstream movement of spawners. Briggs (1953) has observed that winter steelhead ascend the Mad River, Calif., in greatest numbers during periods of temporary high water flows (freshet conditions) accompanied by a brief rise in water temperature.

Shapovalov and Taft (1954) have reported distinct "peak" numbers of steelhead entering Waddell Creek at intervals. Anglers have reported similar occurrences for other streams (Pautzke and Meigs, 1940), but this phenomenon is difficult to detect in creel census studies where angling effort varies with favourable and unfavourable water and weather conditions.

Almost twice as many female as male steelhead were captured from study streams within southern British Columbia. A similar situation prevails within anglers' samples from along the Pacific coast. This sex ratio conflicts with the near 1:1 ratio obtained from trapping studies (Shapovalov and Taft, 1954; Chapman, MS, 1957). Apparently, sport fisheries select for females in anadromous populations of rainbow trout.

Two factors are known to emphasize this observed selectivity. First, frequency of repeat spawning is greater for female steelhead than for males. The slightly greater number of females present in populations because of their greater survival following spawning results in capture of greater numbers of this sex by anglers. Within southern British Columbia repeat spawning was most frequent among steelhead from Cheakamus River; here also the ratio of females to males captured was greatest. Second, males deteriorate in appearance to a greater extent than females as spawning approaches; therefore, greater numbers of males than females are released alive during the later portion of the spawning run.

The high incidence of repeat spawning observed for fish from the Cheakamus River (31.3%) may be a consequence of a contracted term of freshwater residence prior to spawning, as few fish enter the stream to spawn until April 1. Such a thesis assumes that a freshwater existence for adult anadromous trout is more rigorous than is a saltwater existence. This assumption is supported by the observation that within streams of southern British Columbia the incidence of repeat spawning is slightly greater for winter steelhead than summer steelhead. The latter spend the greatest length of time in fresh water prior to spawning.

Idler and Clemens (1959) measured loss of fat, protein, and energy (in calories per kilogram of weight) of sockeye salmon during their spawning migration from the sea to lakes in the upper Fraser River system. Females from both the Chilko and Stuart runs utilized a higher percentage of fats, proteins, and energy reserves than did their male counterparts. This finding agrees with Belding (1934) who determined that the percentage of body weight lost by spawning female Atlantic salmon in the Miramichi River, N.B., was greater than that lost by males. It may be assumed that female steelhead trout similarly lose a greater percentage of body weight during the spawning migration. Therefore, lower survival of males to second or third spawning probably relates to causes other than condition. These other causes are not known precisely, but they may be associated with early stream entry (as at Waddell Creek and within coastal streams of Oregon), a tendency to remain on the spawning grounds for extended periods of time, or fighting in defence of spawning territory.

Mean fork lengths of steelhead populations from streams along the Pacific coast increase from central California to southern British Columbia. This is undoubtedly a consequence of the tendency for steelhead to spend more years in salt water in more northern than southern areas. Marr (1943) observed that older chum and coho salmon from various Pacific coast watersheds are more abundant in northern areas of their range of distribution.

The ratio of years spent in fresh and salt water by steelhead is not constant along the Pacific coast. In all streams except those of south coastal British Columbia, 2-year-old smolts predominate. Numbers of 3-year-old smolts may increase in northern areas although such a trend is not clearly shown in this study.

Some instances (Shapovalov and Taft, 1954; Bali, MS, 1958) of large numbers of 3-year-old smolts have been observed to result from delay of smolt exit by "trapping" through closing of bars at stream mouths in California and southern Oregon. Fish with longer saltwater residence are progressively more abundant in northern areas.

Figure 9 illustrates the manner in which life-history characteristics of steelhead populations vary along the Pacific coast. Change in mean monthly water temperature is included as a possible environmental factor governing population characteristics. The greater mean adult lengths observed among northern steelhead populations is a result of the longer oceanic growing period

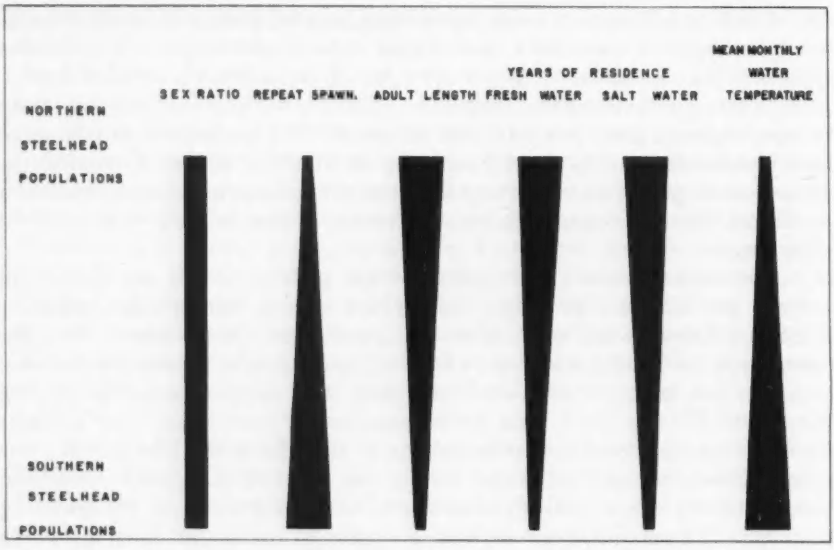

FIG. 9. Schematic representation of changes in life history attributes of steelhead populations, and mean stream temperatures, along the Pacific coast; thick portions of the pointers suggest greatest frequency or amount of an attribute, thin portions, the least.

of these fish. The decrease in frequency of repeat spawning noted for north coastal populations is probably related to the greater number of years which fish of these populations spend in both fresh and salt water. The possibility of survival to subsequent spawning migrations decreases as the age of steelhead increases.

Divergence of characteristics may be related to genetic or environmental influences, or both. Marr (1943) showed that some species of Pacific salmon diverge progressively in some life-history characteristics throughout their range. Svardson (1954) demonstrated that smolt age of Atlantic salmon entering the Baltic Sea increased from south to north. Ricker (MS, 1959) states that the variation which Pacific salmon and steelhead trout exhibit has both a genetic and environmental basis, and "scores of genetically different stocks of a species can exist in one and the same river system, half a dozen or more even within a single lake." This view is supported by Vernon (1957) who has determined that several different races of kokanee exist within Kootenay Lake, B.C., but he has suggested that growth, age at maturity, and morphological differences are genetically controlled.

Elson (1957) and Alm (MS, 1959) have suggested for Atlantic salmon that the age at which smolts migrate to sea is governed by their rate of growth in fresh water. Chapman (1957) has related the age of steelhead smolts at migration to the number of years which they spend in salt water; the youngest (and presumably most rapid growing) smolts spend the shortest periods in salt water. It has been postulated that environmental control of life-history patterns may

operate in steelhead-producing streams which possess headwater lakes (E. Whitesel, personal communication). The moderation of downstream temperatures and water volumes provides a most suitable environment within which steelhead may grow, prior to downstream migration. Differences in stream temperatures along the coast of North America have been demonstrated in this study (Fig. 8). However, other environmental factors which vary geographically may act to regulate growth and migration ages.

Other factors governing changes in steelhead population characteristics along the coast of North America might be the influence of latitudinal changes in day lengths upon feeding habits or pituitary stimulation, or characteristic differences may arise from the action of a combination of several environmental variables related to climatology and the fresh and saltwater environment of the fish.

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APPENDIX 1. Mean fork lengths of winter and summer steelhead in half-monthly intervals for all years of record, 1949–58 (lengths in inches).

	Alouette		Coquitlam		Chehalis		Cheakamus		Capilano		Seymour		Coquihalla	
Time period	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Winter steelhead														
Nov. 1–15														27.25[a]
Nov. 15–30										29.50[a]				
Dec. 1–15	27.00	29.25[a]	25.00[a]	29.75[a]	28.75	29.75				30.50	32.00[a]	29.00[a]		
Dec. 15–31	27.00	26.50	27.00[a]	26.75	30.00	28.00								
Jan. 1–15	30.75	33.25	26.00	29.25	30.25	29.50			28.25[a]	25.50[a]	31.25	28.75[a]	28.75[a]	27.75
Jan. 15–31	26.50	28.25	27.75	27.00	32.25[a]	29.75			28.00[a]	29.50[a]	30.00[a]	28.00[a]	29.75[a]	27.75[a]
Feb. 1–15	30.00	25.25	26.75	26.00	28.00	29.50			28.00	28.25[a]	32.25[a]	29.00		25.75
Feb. 15–28	31.25[a]	29.50		26.50	26.75[a]	29.75			31.00	28.50		27.50	28.00[a]	28.00[a]
Mar. 1–15	35.00[a]	29.50[a]	27.00	28.00	33.00[a]	30.75			30.50	27.50		31.50[a]	32.25[a]	27.50[a]
Mar. 15–31		25.50[a]	27.00	26.50		30.25[a]			31.50	25.00	29.00[a]	29.00	30.25[a]	25.75[a]
Apr. 1–15			26.00[a]	28.50			27.75	29.25	28.75	28.50	28.75	29.00		25.00[a]
Apr. 15–30			22.25	25.50			32.50	36.00	33.00[a]	28.50	28.75[a]	30.50		29.00[a]
Mean length winter steelhead	28.4	26.9	26.60	27.20	29.30	29.50			28.80	28.10	29.30	28.90	28.70	27.00
Summer steelhead														
May 1–15							32.25	30.75	28.00	27.75	33.50	27.75		
May 15–31								29.25	30.00	27.75		29.00		
June 1–15									30.00	28.00	31.25	26.50	29.00[a]	
June 15–30								29.50[a]	28.50	28.75	29.25	26.75	30.75[a]	27.00[a]
July 1–15									29.50	27.25			29.00[a]	27.00
July 15–31									27.00[a]	28.75			28.00	27.00
Aug. 1–15													27.25	25.75
Aug. 15–31													26.00	26.75
Sept. 1–15													25.75	26.75
Sept. 15–30													23.50[a]	24.75
Oct. 1–15									26.00[a]				30.25	27.25
Oct. 15–31													26.25[a]	26.00[a]
Mean length summer steelhead							31.00	30.20	29.20	28.00	30.30	27.50	27.30	26.30

[a]Fewer than five fish in sample.

Protein Nutritive Quality of Commercial Fish Meals as Assessed by Biological and Chemical Methods[1]

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ABSTRACT

Various chemical characteristics of fish meals pertaining to the protein and lipid components were determined and their relation to different biological estimates of protein quality were studied. The results demonstrated the practical importance of selecting appropriate biological assays in order to avoid underestimating or overestimating protein quality. Pepsin digestibility of the crude protein remaining in the meals after chloroform–methanol extraction was significantly correlated with biological estimates of protein quality. Meals of initially high supplementary protein value declined in value to a greater extent than did meals of lower quality. The level of available lysine present in the meals declined with storage but biological tests indicated that a combination of several amino acids rather than any single amino acid was limiting to supplementary protein value.

INTRODUCTION

The results of chemical and biological analyses of the nutritive value of British Columbia whole herring meals were presented in a paper by March et al. (1963). The meals tested in the study reported were composite meals representative of commercial production during different periods over the 1960–61 season. The investigation reported herein was designed to provide further information with regard to the uniformity of quality of individual meals and a limited comparison with anchovy meals and menhaden meals.

FISH MEAL SAMPLES

Twenty-eight samples (Table I) of commercial fish meals were obtained. Of these 21 were herring meals drawn from the production of the eight major reduction plants on the British Columbia coast. Information from the processors indicated that most of the herring meals were whole meals containing solubles

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TABLE I. Description of meals and chemical analysis.

Type of meal	Production date	Code No.	Protein	Ash	Ether extract	Moisture
			%	%	%	%
B. C. herring	Mar.	14	76.2	10.7	9.3	5.1
	Dec.	18	72.6	10.5	12.0	6.1
	Feb.	24	73.2	10.0	8.6	7.5
	Mar.	15	72.3	11.1	10.9	7.5
	Dec.	20	73.2	11.1	11.1	5.5
	Jan.	19	71.9	11.9	11.7	5.6
	Dec.	13	73.1	11.1	9.2	6.7
	Dec.	23	73.1	10.6	9.9	6.7
	Feb.	4	74.7	11.9	8.9	7.3
	Feb.	26	73.4	10.6	13.1	4.0
	Feb.	28	75.8	10.6	8.3	5.8
	Nov.	1	71.6	11.4	10.8	8.7
	Jan.	27	73.8	10.4	9.6	6.6
	Dec.	25	71.8	11.6	8.5	6.1
	Feb.	5	71.1	11.4	10.8	8.7
	Oct.	10	70.9	13.2	6.0	7.8
	Feb.	8	71.8	16.3	10.1	5.1
	Nov.	7	71.9	13.6	10.1	7.2
	Jan.	3	73.5	12.4	7.5	8.0
	Feb.	11	74.2	10.5	7.7	7.5
	Dec.	9	73.4	12.8	8.6	7.1
	Average:		73.0	11.6	9.7	6.7
Anchovy		16	67.5	14.8	–	5.9
		12	68.0	14.8	2.9	7.2
		2	61.9	17.8	4.6	9.8
		6	66.6	17.4	3.7	8.9
		22	65.6	16.3	3.6	6.6
	Average:		65.9	16.2	3.7	7.7
Menhaden		21	64.3	16.3	10.8	7.0
		17	60.2	20.7	10.4	6.9

from the press-water. All the meals were manufactured during the 1960–61 season in the months indicated.

Five South American anchovy meals and two Atlantic coast menhaden meals were included in the survey. These meals were procured in such a way as to ensure that they were from different lots of production. Although no precise information was available as to the date of manufacture it was assumed to be 1960.

The herring meals were all in 100-lb multiwall paper bags. The anchovy meals and one of the menhaden meals were in 100-lb jute bags. The other menhaden meal was shipped in a keg. This latter meal (No. 21) was the only meal labelled as antioxidant-treated (butylated hydroxytoluene). Storage of the meals was under warehouse conditions with no control of temperature.

METHODS

Chemical Analyses

Standard methods (A.O.A.C., 1960) were used for the determination of crude protein, ash, moisture, and ether-extractable fat.

The fat present in fish meals, particularly after meals have been stored, is not completely extractable with diethyl ether. The method of Stansby and Clegg (1955), in which the meal is extracted in two stages with acetone prior to and after acid treatment, was used to extract fat not soluble in diethyl ether. Extraction with acetone was performed subsequent to ether extraction. The amounts of fat extracted sequentially by diethyl ether and the two portions of acetone were determined separately. In an additional analysis for fat the meals were extracted with a 2:1 mixture of chloroform and methanol.

Protein digestibility *in vitro* was measured using pepsin according to the method of Almquist et al. (1935). Digestibility was determined both on the intact meals and on the meals after extraction with chloroform–methanol. The chloroform–methanol extracts of the meals were analyzed for nitrogen. Hot-water-soluble protein was determined using the method of Almquist et al. (1935). Available lysine was estimated chemically by the method of Carpenter (1960). The values obtained from these analyses were calculated as percentages of the meals and as percentages of the crude protein contents of the meals.

Six of the herring meals were reanalyzed after storage for 16 months for ether-soluble fat, chloroform–methanol-soluble fat, pepsin-indigestible protein (on chloroform–methanol extracted samples), and available lysine.

Biological Assays

GROSS PROTEIN VALUES

The procedure of Heiman et al. (1939), with some modification, was followed. The formula of the depletion diet[2] fed during the pre-experimental period was similar to that of Heiman et al. except that it contained vitamin-fortified distillers' dried solubles in place of dried whey, calcium carbonate and tricalcium phosphate in place of oyster shell and bonemeal, and that it was supplemented with manganese sulphate. The reference protein employed was vitamin-free casein. The reference protein and the fishmeals under assay were added to the basal diet to supply 3% of protein as in the original procedure.

New Hampshire pullet chicks from the same breeding stock were used in all tests of gross protein value.

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[2]The composition of the depletion diet per 100 lb was as follows: ground yellow corn 30.8, ground wheat 8.04, bran 12.06, dextrose 29.8, calcium carbonate 0.25, tricalcium phosphate 2.20, iodized salt 0.46, vitamin-fortified distillers' dried solubles 2.07, dehydrated cereal grass 4.01, feeding oil (2250 USP units vitamin A, 300 ICU vitamin D_3 per gram) 0.26 lb and manganese sulphate 6.0 g. In the experimental diets the amount of tricalcium phosphate included in the diet was adjusted according to the mineral content of the fishmeal. The total weight of the diet was adjusted to 100 lb with dextrose.

The formula of the breeder diet was unchanged during the entire period that chicks were required for these tests, and for the supplementary protein value tests described later.

The chicks were fed the depletion diet from 0–2 weeks of age. At 2 weeks of age they were weighed, the chicks of extreme weight discarded, and the remainder distributed into groups of 15 chicks. Each experimental diet was fed *ad libitum* to three replicate groups for 3 weeks. The reference protein was fed to three replicate groups of chicks in each test. Two estimates of gross protein value (G.P.V.) were calculated as follows:

$$\text{G.P.V.}_{\text{weight gain}} = \frac{\text{average weight gain of chicks fed diet with fishmeal}}{\text{average weight gain of chicks fed diet with reference protein}} \times 100$$

$$\text{G.P.V.}_{\text{diet efficiency}} = \frac{\text{body weight gain/feed consumed (chicks fed fishmeal)}}{\text{body weight gain/feed consumed (chicks fed reference protein)}} \times 100$$

SUPPLEMENTARY PROTEIN VALUE

In this assay procedure for the assessment of protein quality, the protein concentrates were each fed as the sole source of supplementary protein in a practical type chick starting diet.[3] The reference protein employed was isolated soybean protein supplemented with 3.33% of DL-methionine. The reference protein and the respective fishmeals were added to the basal diet to supply 8% of protein.

New Hampshire cockerel chicks from the breeding stock described above were used in all tests of supplementary protein value. The chicks were fed a chick starting ration for 3 days and were then distributed at random into groups of 18 chicks. Each experimental diet was fed *ad libitum* to three replicate groups for 3–4 weeks. The reference protein was fed to three replicate groups of chicks in each test.

As in the case of the gross protein values, supplementary protein values were estimated on the basis of the growth response obtained with the diet containing fish meal relative to that obtained with the diet containing the reference protein, and on the basis of the relative efficiency of diet utilization.

$$\text{S.P.V.}_{\text{body weight}} = \frac{\text{average weight of chicks fed diet with fish meal}}{\text{average weight of chicks fed diet with reference protein}} \times 100$$

$$\text{S.P.V.}_{\text{diet efficiency}} = \frac{\text{body weight gain/feed consumed (chicks fed test fishmeal)}}{\text{body weight gain/feed consumed (chicks fed reference protein)}} \times 100$$

DETERMINATION OF LIMITING AMINO ACIDS IN STORED HERRING MEAL

Three experiments were conducted to determine the growth response to supplementation of the S.P.V. diet containing stored herring meals with various amino acids, singly and in combination. In experiment 1, meals 24, 8,

[3]The composition of the basal diet used in the test was as follows: ground wheat 85.0 lb, limestone 1.25 lb, bonemeal 2.0 lb, and iodized salt 0.5 lb per 100 lb; manganese sulphate 60 mg, menadione 0.22 mg, riboflavin 1.3 mg, folacin 0.25 mg, choline chloride 600 mg, α-tocopherol acetate 6.0 mg, vitamin B_{12} 6.0 μg, vitamin A 2000 USP units and vitamin D_3 120 ICU per lb. The amount of bonemeal included in the diet was adjusted according to the mineral content of the fishmeal. The total weight of the diet was adjusted to 100 lb with dextrose.

and 9 were the herring meals included in the S.P.V. diet. These meals were chosen as representative of meals which originally had divergent S.P.V.$_{\text{body weight}}$'s (138, 124, and 117, respectively). The New Hampshire pullet chicks used in the experiment were fed a practical chick starter for 5 days, then randomized into lots of 16 chicks and put on test when they were 6 days old. Duplicate lots were fed each experimental diet *ad libitum* to 32 days of age.

For experiments 2 and 3 a composite sample of equal parts of meals 4, 13, 15, 18, 19, 20, 23, and 26 was prepared. These meals initially had S.P.V.$_{\text{body weight}}$'s within a narrow range (139 to 132). The composite meal was used as the protein supplement in the S.P.V. diet. In experiments 2 and 3 both New Hampshire and White Leghorn cockerel chicks were used. Chicks of two different breeds were used because it has been found that diets varying slightly in amino acid composition may rank differently in the growth rate they support depending upon the genetic background of the chicks (March et al., 1965a). As before, the chicks were fed a practical chick starter for 3–4 days before being randomized into the experimental lots. Triplicate lots of chicks of each breed were fed each diet *ad libitum* during the experiments.

The amino acids used in the various experimental diets for the three experiments and other details are shown with the results in Table VIII. The levels of the individual amino acids added to the diets were lysine 0.2, arginine 0.2, histidine 0.04, and methionine 0.2%.

RESULTS AND DISCUSSION

Chemical Analyses

The proximate analyses of the fish meals studied are shown in Table I. The meals are listed here and in subsequent tables in descending order of the values for S.P.V.$_{\text{body weight}}$ within each type. Because the meals were made from whole fish, the composition of the meals of each type (herring, anchovy, and menhaden) was quite consistent. The crude protein content of the herring meals ranged from 70.9 to 76.2% (average 73.0), the menhaden meals from 61.9 to 68.0% (average 65.9), and that of the two menhaden meals was 60.2 and 64.3%. The percentage of ash in the herring meals was consistently lower, 10.0–13.6% (average 11.6) than in the anchovy meals (average 16.2). The two menhaden meals contained 16.3 and 20.7%, respectively. Ether-extractable lipid ranged from 6.0 to 13.1% (average 9.7) of the herring meals, and from 2.9 to 4.6% (average 3.7) of the anchovy meals. The menhaden meals contained 10.4 and 10.8% of ether-extractable fat, respectively. The moisture content of the herring meals ranged from 4.0 to 8.7% (average 6.7), of the anchovy meals from 5.9 to 9.8% (average 7.7), and the menhaden meals contained 6.9 and 7.0%, respectively. The average total of the percentages of crude protein, ash, ether extract, and moisture was 101% for the herring meals, only 94% for the anchovy meals, and 98% for the menhaden meals.

The low values obtained by totalling the results of the proximate analysis of the anchovy meals are due to the fact that the fat was poorly extracted

from the anchovy meals by diethyl ether. The fat present in the anchovy meals was evidently oxidized to a greater extent than in the other meals. A relatively high proportion of the anchovy meal fat was extracted by acetone before and after acid hydrolysis.

The extractability of the lipids from the meals with different solvents is given in Table II. The ether-extractable lipids made up a larger proportion of

TABLE II. Extractability of lipids with different solvents.

Type of meal	Code No.	Diethyl ether extract	First acetone extract	Second acetone extract	Total ether and acetone extracts	Chloroform–methanol extract	Ratio of ether extract: chloroform-methanol extract × 100
		%	%	%	%	%	
B.C. herring	14	9.3	1.28	1.32	11.9	16.3	57
	18	12.0	1.08	1.32	14.4	18.5	65
	24	8.6	2.40	1.38	12.4	16.8	51
	15	10.9	1.16	1.16	13.2	17.3	63
	20	11.1	1.56	2.35	15.0	17.5	63
	19	11.7	2.05	1.96	15.7	18.1	65
	13	9.2	1.07	1.30	11.6	16.8	55
	23	9.9	1.49	1.95	13.3	17.2	58
	4	8.9	0.77	1.90	11.6	13.6	65
	26	13.1	2.98	1.78	17.9	22.4	58
	28	8.3	1.18	1.70	11.2	14.2	58
	1	10.8	0.73	1.52	13.0	17.4	62
	27	9.6	1.30	1.68	12.6	16.9	57
	25	8.5	2.09	1.92	12.5	18.3	46
	5	10.8	0.76	1.04	12.6	15.9	68
	10	6.0	0.59	1.67	8.3	10.5	57
	8	10.1	0.92	1.24	12.3	18.5	55
	7	10.1	0.73	1.30	12.1	18.0	56
	3	7.5	0.68	1.10	9.3	14.5	52
	11	7.7	0.65	1.82	10.2	13.2	58
	9	7.6	0.92	1.20	10.7	18.0	42
Anchovy	16	–	0.97	1.30	–	11.5	–
	12	2.9[1]	0.69	2.47	6.1	10.1	29
	2	4.6	1.24	4.90	10.7	11.0	42
	6	3.7	1.28	1.51	6.5	11.7	32
	22	3.6	2.49	3.70	9.8	13.1	27
Menhaden	21	10.8	1.45	2.21	14.5	15.9	68
	17	10.4	1.32	1.15	12.9	14.9	70

the chloroform–methanol soluble lipids in the herring and menhaden meals than in the anchovy meals. This is of significance probably only as an indication of the lesser amount of free fat as compared with the amounts of complex lipids present in the anchovy meal.

The chloroform–methanol extracts were considerably higher than the combined ether and acetone extracts. The difference is due to the fact that

chloroform–methanol extracts complex lipids and non-lipid material not appreciably soluble in ether or acetone. This is indicated by the amount of nitrogen present in the chloroform–methanol extracts (Table III). If chloroform–methanol is used as a solvent for extracting fat in the proximate analysis of fish meal it is necessary to remove the nonlipid fraction from the extract.

TABLE III. Partition of crude protein nitrogen.

		Pepsin-indigestible protein:			Percentage of total nitrogen present as:		
Type of meal	Code No.	In intact meal	In chloroform–methanol extracted meal		Chloroform-methanol soluble	Hot-water-soluble	Available lysine
B.C. Herring	14	6.2	5.1	(5.5)[a]	7.0	8.0	6.0
	18	6.7	4.9	(5.3)	7.9	8.5	6.5
	24	7.2	–	–	7.2	9.2	5.9
	15	6.9	4.7	(5.1)	7.8	7.8	6.0
	20	7.0	4.8	(5.1)	6.9	7.6	6.4
	19	6.2	4.5	(4.9)	7.0	7.5	6.4
	13	8.3	5.7	(6.3)	8.7	7.2	6.6
	23	6.9	4.8	(5.2)	8.3	8.5	6.7
	4	5.8	4.9	(5.1)	3.6	5.1	6.4
	26	7.1	5.4	(6.0)	8.7	10.6	6.3
	28	7.8	5.8	(6.1)	4.6	7.4	6.1
	1	6.6	5.1	(5.5)	7.1	8.1	6.6
	27	7.1	5.3	(5.7)	7.4	8.5	6.2
	25	7.8	5.2	(5.7)	10.3	8.7	6.1
	5	6.0	4.9	(5.1)	4.9	6.2	6.7
	10	7.3	5.8	(6.0)	3.1	5.4	7.5
	8	7.1	5.7	(6.3)	9.8	9.4	6.1
	7	7.2	5.0	(5.5)	8.7	7.7	6.8
	3	7.6	5.6	(6.0)	6.8	7.6	6.6
	11	8.5	6.6	(6.9)	4.3	4.9	6.7
	9	6.4	4.6	(5.2)	10.9	10.9	6.3
Anchovy	16	9.8	7.5	(7.8)	4.0	4.9	6.9
	12	9.7	7.4	(7.7)	3.9	6.0	6.8
	2	14.7	11.0	(11.3)	3.2	4.9	6.0
	6	11.9	8.5	(9.0)	6.0	5.1	5.8
	22	13.4	10.1	(11.0)	7.8	7.2	5.8
Menhaden	21	7.0	–	–	5.8	10.3	6.6
	17	7.2	5.7	(6.0)	5.5	8.5	6.5

[a]Pepsin-indigestible protein nitrogen in chloroform–methanol extracted meal calculated as a percentage of the total nitrogen minus chloroform–methanol extractable nitrogen.

Table III shows the values obtained for indigestible protein, chloroform–methanol-extractable nitrogen, hot-water-soluble protein, and available lysine. Some of the meals were tested for pepsin digestibility using the intact meal. The values obtained in this way indicated lower digestibility than those obtained when the meals were extracted with chloroform–methanol prior to enzyme treatment. The differences between the values obtained on the intact

meal and the extracted meals are attributed to (a) the physical barrier to enzyme action presented by the lipid present in the intact meal and (b) to a portion of the nitrogen extracted by chloroform–methanol which may not have been brought into aqueous solution by treatment with pepsin.

Because of the difficulty in assessing digestibility of protein associated with lipid on the basis of *in vitro* testing, pepsin digestibility was determined on chloroform–methanol-extracted samples of the meals and the results calculated on the basis of the total crude protein and on the total crude protein minus the crude protein extracted by the chloroform–methanol. The herring meals generally contained less pepsin-indigestible protein than did the samples of anchovy meal tested. This was true whether the indigestible protein was determined on the original meals and expressed as a percentage of the total crude protein in the meal or determined on the chloroform–methanol extracted meal and expressed on the basis of the amount of crude protein in the extracted meal.

The percentage of hot-water-soluble protein present in the total crude protein of the meals varied considerably among the meals. Since the meals were all derived from whole fish the variation does not reflect differences in the composition of the raw material as it does in the case of meat meals or of fish meals processed from scrap. Rather it is attributable to differences in the solubilization of the protein during cooking and subsequent loss into the presswater, or differences due to the fact that some of the meals had presswater added back during processing.

The values for available lysine in the meals ranged from 5.8 to 7.5% of the total crude protein. There did not appear to be any general difference in the available lysine content of meals from different species of fish. Pritchard et al. (1964) reported that Peruvian fish meals, which were made mainly from anchovy, were quite variable in available lysine. Twenty-five samples of Peruvian meal contained from 4.7 to 7.7% of available lysine in the protein. Eighty-seven samples of herring meals assayed in the same survey contained from 5.5 to 8.1% of available lysine in the protein. In view of the decline in available lysine during storage of meals noted in the present report, it seems likely that differences in available lysine found among commercial samples of fish meals made from uniform raw material may frequently be the result of differences in storage time and temperature.

Biological Assays

The results of the initial biological tests are given in Table IV. The ranges of values obtained from the results of the biological tests of all meals were in declining order as follows: $S.P.V._{\text{body wt.}}$ (range 44 units), $G.P.V._{\text{wt. gain}}$ (range 37 units), $G.P.V._{\text{diet efficiency}}$ (range 22 units), and $S.P.V._{\text{diet efficiency}}$ (range 23 units or 13 units exclusive of meal 19). The average values for the herring meals and the anchovy meals were similar in the case of $G.P.V._{\text{wt. gain}}$ and $G.P.V._{\text{diet efficiency}}$. Average $S.P.V._{\text{body wt.}}$ and $S.P.V._{\text{diet efficiency}}$ were higher

TABLE IV. Relative nutritive quality of fish meals as estimated by different biological tests.

Meal No.	S.P.V. weight gain	S.P.V. diet efficiency	G.P.V. weight gain	G.P.V. diet efficiency
Herring meal				
14	142	109	104	96
18	139	113	111	102
24	138	110	94	97
15	136	110	108	98
20	136	113	95	94
19	135	123	97	94
13	135	109	91	93
23	134	107	99	98
4	134	109	97	104
26	132	107	85	92
28	129	111	104	99
1	128	109	114	113
27	128	108	100	103
25	127	109	98	98
5	127	112	101	104
10	126	108	98	96
8	124	107	92	99
7	121	107	100	103
3	121	106	94	99
11	118	106	89	98
9	117	105	91	103
Average:	130	109	98	99
Anchovy meal				
16	125	105	115	99
12	124	103	101	105
2	116	103	100	106
6	113	103	98	102
22	108	100	78	86
Average:	117	103	98	100
Menhaden meal				
21	134	107	91	91
17	127	108	111	99

for the herring meals than for the anchovy meals. Table V shows the correlation coefficients between the biological values of the meals as estimated in different ways. The correlations between the different measures of biological response and the available lysine content of the fish meal protein, the *in vitro* estimates of digestibility, and the relative solubility of the fish meal lipids in diethyl ether and in chloroform–methanol are also presented.

Two sets of correlation coefficients were calculated. One set included the various values for all of the fishmeals and a second set only the herring meals. The correlation coefficients were calculated on the values for the herring meals separately to avoid fallacious conclusions which might be drawn from differences in the composition of meals derived from different species of fish. Meals procured from different species of fish may vary in biological value for reasons unrelated to the differences in analytical values being compared.

TABLE V. Correlation coefficients between different biological estimates of nutritive value and chemical analysis.

	GPVW[a]	GPVE	SPVW	SPVE	LYS	IP/CP	IP/C-E	E/CM
All meals								
GPVW	1.000							
GPVE	0.603[c]	1.000						
SPVW	0.314	−0.130	1.000					
SPVE	0.251	−0.058	0.677[c]	1.000				
LYS	0.221	0.133	0.075	0.086	1.000			
IP/CP	−0.214	−0.070	−0.694[c]	−0.660[c]	−0.287	1.000		
IP/C-E	−0.250	−0.096	−0.706[c]	−0.674[c]	−0.320	0.997[c]	1.000	
E/CM	0.399[b]	0.016	0.672[c]	0.677[c]	0.347	−0.719[c]	−0.744[c]	1.000
Herring meals								
GPVW	1.000							
GPVE	0.578[c]	1.000						
SPVW	0.329	−0.331	1.000					
SPVE	0.269	−0.201	0.506[b]	1.000				
LYS	−0.025	−0.097	−0.353	−0.108	1.000			
IP/CP	−0.360	−0.188	−0.411	−0.436	0.238	1.000		
IP/C-E	−0.437	−0.232	−0.434	−0.492[b]	0.139	0.969[c]	1.000	
E/CM	0.431	0.117	0.446[b]	0.554[b]	0.196	−0.206	−0.350	1.000

[a]GPVW: gross protein value (weight gain); GPVE: gross protein value (diet efficiency); SPVW: supplementary protein value (weight gain); SPVE: supplementary protein value (diet efficiency); LYS: available lysine, per cent of crude protein; IP/CP: pepsin-indigestible protein in chloroform-methanol extracted meal expressed as a percentage of total crude protein in the original meal; IP/C-E: pepsin-indigestible protein in chloroform methanol extracted meal expressed as a percentage of crude protein minus chloroform-methanol-extractable protein; E/CM: ether-extractable fat, per cent of chloroform-methanol-extractable fat.

[b]Significant at 5% level.

[c]Significant at 1% level.

The estimates of G.P.V. based on weight gain and diet efficiency were significantly correlated, as were the respective estimates of S.P.V. The correlations between S.P.V. and G.P.V. were not statistically significant on the basis of either weight gain or diet efficiency. A high degree of correlation might normally be expected between estimates of protein quality based upon growth response and upon efficiency of feed conversion.

The lack of correlation between S.P.V. and G.P.V. estimates of protein quality indicates the importance of designing biological assays of protein quality to evaluate quality specifically for the function for which the protein may be expected to be utilized. In these particular tests, for example, some samples of fishmeal gave favourable results when tested to supply 8% of protein in a total of 20% dietary protein, but not when tested to supply 3% in a total of 11%. Grace and Richards (1964), in a study of the biological value of meat meals, found no significant correlation between the results obtained by the G.P.V. method and by a method of determining relative nutritive values from a six-point bioassay in which the basal diet was similar to that used in the G.P.V. method but in which the meat meals were included to give

protein levels of 11, 15, and 20%. They concluded that the results obtained regarding protein quality of a supplement by a method employing a suboptimal level of protein may not give an accurate indication of the quality which the supplement might exhibit with a practical level of protein in the diet. It is obvious, too, that the ingredients comprising the diet to which the fishmeal is added will also determine the adequacy of the fishmeal as a source of amino acid. For example Bird et al. (1965) fed fishmeals to chicks to supplement a corn-soy and a corn-soy-cottonseed basal diet, respectively, and showed that the relative supplementary value of the fishmeals varied between the two basal diets.

None of the biological estimates of protein quality was significantly correlated with the levels of available lysine as determined chemically in the meals. It was expected from the results reported by other investigators (Carpenter et al., 1957; Boyne et al., 1961; Grace and Richards, 1964) that there would have been a correlation with G.P.V. It may be in the case of the fishmeals included in the present survey that the level of available lysine was sufficiently high, and the uniformity of the meals such, that the amount of available lysine present was in only a few instances a growth-limiting factor in the G.P.V. test. Duckworth et al. (1961), in an extensive survey of the protein concentrates by a modification of the G.P.V. method, found that of the various concentrates tested, fishmeals ranked the highest in quality with a concentration of samples at the upper end of the range of values obtained. This concentration of values at the upper end of the range was due to the uniformly high quality of the herring meals which constituted 10 of the total 20 samples of fishmeal tested. The lack of correlation between the results of the S.P.V. method of evaluation and levels of available lysine are explainable on the basis that with a 20% protein diet in which 8% of protein is contributed from fishmeal the amount of lysine in the diet is unlikely to be limiting even when the availability of lysine in the herring meal is relatively low. Grace and Richards (1964) noted that although the level of available lysine correlated well with the G.P.V. of the meat meals tested, there was no correlation with the relative protein value. As a product made from the entire fish, herring meal should normally contain sufficient lysine to meet the requirement under the conditions of the S.P.V. method. If, because of adverse processing conditions, or storage, the level of available lysine is reduced, the availability of some other amino acids may likewise decline so that lysine still does not become the primary limiting amino acid. A biological assay in which protein concentrates are tested as supplements in a 20% protein diet, therefore, may be considered to represent a test somewhere between the G.P.V. method and methods in which the protein tested supplies the only protein in the diet. Using the latter method it has been shown that the growth response to herring meal protein is not limited by the amount of available lysine present. Miller (1956), for example, found methionine to be the limiting amino acid in overheated fishmeals. Laksesvela (1958) studied the effect of high temperature on the biological availability of the amino acids in herring meal. He reported

that in meal in which heating produced a 40% loss in available lysine, lysine was nevertheless not the primary limiting amino acid when the meal was fed to chicks as the sole source of protein at a level to supply 10% of protein in the diet. Neither was a combination of lysine and methionine an effective supplement in this instance. Histidine appeared to have been critically affected. Njaa (1961) showed that when herring meal is fed to rats as the sole source of protein, the utilization of the protein can be improved by supplementation of the diet with methionine or cystine. Lysine, valine and tryptophan were without effect when tested alone or in combination with methionine.

Njaa (1961) concluded that methionine and cystine are the first limiting factors in herring protein. He reported that the effects of graded amounts of methionine used to supplement herring meal fed to rats were greater than would be expected on the basis of the requirement of the rat for methionine and cystine. The explanation offered by Njaa is that herring meal contains pools of sulphur-amino acids with different rates of utilization. Those which are utilized relatively slowly may be drawn upon to a decreasing extent as supplementation with methionine is increased. The results of a study on the effect of heating on pork protein (Donoso et al., 1962) is interesting in this connection. They found that following heat treatment of the protein there was a decline in the net utilization which, in the case of lysine was due to lowered digestibility, but which, in the case of the sulphur amino acids, was due to the fact that although they were absorbed they were not available for protein synthesis.

Pepsin digestibility of the fish meal protein was correlated with the biological estimates of quality in varying degree, dependent upon whether the indigestible nitrogen was calculated as a percentage of the total nitrogen minus the chloroform–methanol-extractable nitrogen and the particular biological estimate, and whether all meals or only herring meals were compared. On the basis of the digestibility based on total nitrogen present there was no correlation with either G.P.V. estimate. When all of the fishmeals were compared the correlation was highly significant with either estimate of S.P.V., but was not significant with the herring meals alone. Correlation of indigestible nitrogen based on total nitrogen minus chloroform–methanol-extractable nitrogen was highly significant with S.P.V. estimates with all meals tested. When the herring meals alone were considered, the correlation was significant only with $S.P.V._{\text{diet efficiency}}$. The correlations were not significant with G.P.V. estimates of biological quality.

The digestibility of the protein based on total nitrogen minus chloroform–methanol-extractable nitrogen appeared to give fairly consistent correlation with biological value as estimated by either $S.P.V._{\text{body weight}}$ or $S.P.V._{\text{diet efficiency}}$.

The amounts of hot-water-soluble crude protein and chloroform–methanol-soluble crude protein present in the meals were significantly correlated ($r = 0.74$, $p < 0.01$). Although experiments were not performed to check the possibility, it would appear that pepsin digestibility of the crude protein remaining after chloroform–methanol extraction provides an estimate of the

availability of the amino acids present in the better balanced proteins of the meal. By the present methods used in determining pepsin digestibility, low digestibility of heat- or storage-damaged protein could be obscured by the presence of relatively large amounts of soluble crude protein. Lovern (1965) recently evaluated various methods used in determining pepsin digestibility of protein and emphasized the fact that most procedures actually measure solubilization. He suggested that a test in which the extent of peptide bond hydrolysis would be measured might be developed which would be applicable to both water-soluble and insoluble protein material.

Thurston et al. (1960) compared pepsin digestibility (A.O.A.C.) and growth response of chicks to fishmeals used to provide 20% protein as the sole source of protein in a diet composed of purified ingredients and concluded that there was little relationship except when both were distinctly low in an obviously scorched meal. In the present test there was no significant correlation with the meals tested between the amount of available lysine and the pepsin digestibility of the protein. This is in agreement with the findings of Olley and Watson (1961) and Snyder et al. (1962).

The correlations of the proportions of chloroform–methanol extractable fat present in the meals which were soluble in diethyl ether (E/CM) with the results of other determinations were also measured. There were significant correlations when all the meals were considered with $G.P.V._{\text{weight gain}}$, $S.P.V._{\text{body weight}}$, $S.P.V._{\text{diet efficiency}}$, and with the pepsin digestibility of the protein. When only the herring meals were considered E/CM was significantly correlated with $G.P.V._{\text{weight gain}}$, $S.P.V._{\text{diet efficiency}}$ and protein digestibility of crude protein minus chloroform–methanol extractable protein. The differences in correlations, depending upon whether all of the meals or only the herring meals were considered, was occasioned by the fact that the anchovy meals as a group were relatively low in fat but higher in indigestible protein.

Potter et al. (1962) determined the metabolizable energy values for the chick and the coefficients of digestibility of the protein and fat in menhaden meal. From their results there did not appear to be any correlation between the percentage of the total fat which was ether-extractable and the digestibility coefficient of the fat in the meals. One point which may be noted in connection with their data is that two of the six meals under test showed relatively poor digestibility of both the fat and the protein fractions.

The association between oxidative changes in the oil present in fishmeal and a decline in protein nutritive value has been the subject of a great deal of research. Biely et al. (1955) studied the nutritive value of a series of specially prepared herring meals including low-fat meals which had been hexane-extracted. Under the conditions of the experiment the presence of oil in the meals did not appreciably affect the growth response of chicks to either freshly prepared or to stored meals when the basal diet was adequately supplemented with vitamins. The possibility that the biological test employed may not have been sufficiently sensitive to detect small differences in protein quality is suggested by the results of more recent experiments. Lea et al. (1958) showed

that the level of available lysine in herring meal did not decline during storage if the meal was defatted or stored in nitrogen. Rand et al. (1960) stored samples of commercial fishmeal and of defatted meal and noted a decrease in protein quality in several of the commercial meals, but not in the defatted meal, when the meals were fed to chicks as the only source of dietary protein. More recently, Moorjani et al. (1965) compared the protein quality of fish flours made from freshly manufactured sardine meal and from sardine meal stored for 2 months at 28–33 C. When the flours were fed to rats to supplement a methionine-deficient diet the flour made from the stored meal was inferior to that made from fresh meal. Available lysine, cystine, and methionine were somewhat lower in flour made from stored meal. The authors consider oxidation of lipids in fish meal to be a factor in the lower nutritive value of flour prepared from stored meal. March et al. (1965b) found that antioxidant treatment of herring meal prior to storage had a stabilizing effect on the metabolizable energy and the S.P.V. for the chick. It was not determined whether the effect of antioxidant on S.P.V. was direct or indirect through stabilization of the fat present in the meal.

Table VI lists the $S.P.V._{\text{body weight}}$ of the meals as originally determined and after storage for the indicated periods.

Estimates of protein quality according to $S.P.V._{\text{body weight}}$ of herring meals which had been stored for 10–21 months lay within a narrower range than did the original determinations. Those meals which initially had values of over 125 declined in value. After approximately 12 months there seemed little tendency for further deterioration. Meals of original low $S.P.V._{\text{body weight}}$ did not decline appreciably in value. Anchovy meals of relatively good quality dropped considerably in nutritive value, but a meal which had shown very poor quality remained unchanged. Similarly, in the case of the menhaden meals, the one of higher initial quality declined in value, whereas the one of lower quality showed less change.

The six herring meals listed in Table VII were selected for analysis because they represented a wide range of $S.P.V._{\text{body weight}}$'s when they were first assayed. All the meals showed a decrease in available lysine during storage which averaged 25% of the original content. Available lysine levels were not related to the $S.P.V._{\text{body weight}}$'s before or after storage. In some meals the amount of ether-extractable lipid declined during storage, both as a percentage of the meal and as a percentage of the chloroform–methanol extractable lipid. The effect of storage was not consistent in this regard, extractability of lipids from two of the meals remaining relatively unchanged during storage. The percentage of nitrogen extracted with chloroform–methanol after storage of the meals was generally similar to that obtained in the original determination. Pepsin digestibility of the protein was lower after storage.

Determination of Limiting Amino Acids in Stored Herring Meal

Table VIII shows the average weights of chicks in experiments designed to determine which amino acid or acids were limiting in the herring meals

TABLE VI. Supplementary protein values (weight gain) of fish meals stored for different lengths of time.

Meal No.	Storage time (*months*)	S.P.V.	Storage time (*months*)	S.P.V.	Storage time (*months*)	S.P.V.	Storage time (*months*)	S.P.V.
Herring meal								
14	3	142	10	121	13	117	18	119
18	6	139	15	120	16	125		
24	5	138	12	124	18	119		
15	3	136	13	114				
20	6	136						
19	4.5	135						
13	6	135						
23	7	134	16	118				
4	2	134	13	117	19	122		
26	5	132	11	126	19	120		
28	5	129						
1	5	128	17	119				
27	6	128						
25	5	127	14	117				
5	2	127						
10	7	126	18	123				
8	3	124	13	123				
7	5.5	121						
3	3	121	14	115				
11	3	118	13	112	19	114		
9	5	117	13	118	21	118		
Anchovy								
16	?	125	?+9	111				
12	?	124	?+11	115				
2	?	116						
6	?	113						
22	?	108	?+6	105				
Menhaden								
21	?	134	?+9	114				
17	?	127	?+7	124				

after storage. Despite the considerable decrease in the amount of available lysine present in the meals during storage (Table VII), supplementation of the meals with lysine by itself did not consistently improve the biological value when the meals were fed to supply 8% of protein in a diet containing a total of 20% protein. Of the three meals which were treated individually in experiment 1, No. 24 and 8 were improved by the addition of a combination of lysine and methionine. Meal No. 9, which was of poor quality at the outset of the experiment, was not benefitted by the addition of lysine and methionine.

The lack of response of meal No. 9 to lysine and methionine supplementation, as opposed to the positive response obtained in the case of the other two meals, is similar to the results reported by Anwar (1965) from amino acid supplementation of fish meal and meat meal. Anwar found that autoclaving experimentally prepared freeze-dried meals reduced the available lysine content and the G.P.V. Supplementation of the autoclaved meals with lysine

TABLE VII. Comparison of changes in some characteristics of herring meals during storage.

Meal No.	S.P.V.		Available lysine (in protein)		Ether extract		Chloroform–methanol extract		Ether extract of chloroform methanol extract		Chloroform–methanol soluble nitrogen[b]		Pepsin-indigestible nitrogen[c]	
	Orig.[a]	Stored[a]	Orig.	Stored	Orig.	Stored	Orig.	Stored	Orig.	Stored	Orig.	Stored	Orig.	Stored
			%	%	%	%	%	%	%	%	%	%	%	%
14	142 (3)	119 (18)	6.0	4.6	9.3	7.4	16.3	15.6	57	47	7.0	7.4	5.5	6.2
24	138 (5)	119 (18)	5.9	4.7	8.6	8.1	16.8	15.9	51	51	7.2	7.0	–	6.2
4	134 (2)	122 (19)	6.4	5.0	8.9	8.4	13.6	14.2	65	59	3.6	5.0	5.1	6.1
26	132 (5)	120 (19)	6.3	4.5	13.1	13.2	22.4	21.6	58	61	8.7	8.7	6.0	6.7
11	118 (3)	114 (19)	6.7	4.7	7.7	6.1	13.2	12.5	58	49	4.3	4.3	6.9	7.4
9	117 (5)	118 (21)	6.3	4.4	8.6	6.3	18.0	17.1	48	37	10.9	10.5	5.2	5.3

[a]Age of meals, months.
[b]Percentage of total nitrogen.
[c]Percentage of total nitrogen-minus chloroform–methanol extracted nitrogen.

TABLE VIII. Response of chicks fed diets containing various herring meals to supplementation with several amino acids singly and in combination.

Description of meal	Average weight of chicks	
	g	g
Experiment 1[a]	N.H.	
No. 24 — stored 23 months unsupplemented	366	
+ lysine	366	
+ methionine	367	
+ lysine and methionine	393[d]	
No. 8 — stored 23 months unsupplemented	341	
+ lysine + methionine	380[d]	
No. 9 — stored 24 months unsupplemented	365	
+ lysine + methionine	349	
Experiment 2[b]	N.H.	W.L.
Composite sample of meals — stored 26 months unsupplemented	405	368
+ lysine	419	390[d]
+ arginine	412	
+ histidine	410	377
+ methionine	408	386
+ lysine + methionine	419	396
+ arginine + methionine	424	
+ histidine + methionine	414	
+ lysine + arginine + methionine	429	
+ lysine + arginine + methionine + histidine	415	407[d]
+ glycine[f]	411	
Newly manufactured meal unsupplemented	406	375
+ lysine + methionine	423	395
Experiment 3[c]		
Composite sample of meals — stored 28 months unsupplemented	375	350
+ lysine	367	363
+ methionine	370	346
+ lysine + methionine	386[d]	358
+ arginine	372	359
+ arginine + methionine	387[d]	365[d]
+ lysine + arginine + methionine	395[e]	375[e]

[a]Experiment 1: average of duplicate lots of 16 New Hampshire pullets at 32 days of age.
[b]Experiment 2: average of triplicate lots of 18 New Hampshire cockerels and triplicate lots of 18 White Leghorn cockerels at 28 days of age.
[c]Experiment 3: average of triplicate lots of 18 New Hampshire cockerels and triplicate lots of 18 White Leghorn cockerels at 31 days of age.
[d]Significant at 5% level.
[e]Significant at 1% level.
[f]Glycine added to supply nitrogen equivalent to that from lysine + arginine + methionine + histidine in the previous treatment.

restored the G.P.V. to approximately that of the control, provided the nutritive value had not been too greatly impaired. Similarly, in the case of commercially manufactured meals, supplementation with lysine raised the G.P.V. of only those meals which were relatively high in lysine.

The composite sample of the meals prepared for experiments 2 and 3 represented meals which had been stored an average of 26–28 months. Supplementation with lysine alone resulted in an improvement in growth only in experiment 2, and the improvement was statistically significant only with

the White Leghorn chicks. No significant response was noted to supplementation with arginine, histidine, or methionine added singly to the composite meal. Combinations of either lysine or arginine with methionine, or of all three amino acids, used to supplement the composite meal, gave an improvement in growth which was specifically due to these essential amino acids because the addition of lysine was without effect in experiment 2.

The sample of newly manufactured meal which was included in experiment 2 showed some improvement from the addition of lysine and methionine. It is interesting to note that growth with this newly manufactured meal was similar to that with the composite sample of stored meals although some of the meals comprising the composite sample were known to have deteriorated during storage. Accordingly, it may be assumed that the fresh meal was of only average quality.

It is notable that whereas meals which were analyzed for available lysine before and after storage showed a decline averaging 25% in available lysine, lysine was evidently not the primary limiting amino acid in the stored meals under the conditions of testing for $S.P.V._{\text{body weight}}$.

CONCLUSIONS

Conclusions regarding the relative protein nutritive value of different samples of fishmeal based on biological tests will depend upon the type of diet which is employed in the assay. In the present survey the correlation was poor between the results of gross protein values determined with diets in which the fishmeal supplied 3% of supplementary protein to a total dietary protein of 11% and supplementary protein values determined with diets in which the fishmeal supplied 8% of supplementary protein to a total of 20%. The available lysine content of the meals at the time the protein quality was compared by the two biological assays was not significantly correlated with the values obtained by either method of assay. This was attributed to the relatively high and uniform levels of available lysine present in the meals. Pepsin digestibility measured by a method employing an excess of the enzyme was correlated with the biological estimates of protein quality. The highest correlation between pepsin digestibility and biological value was obtained on chloroform–methanol-extracted meal with per cent digestibility based on the total nitrogen minus that extracted by the solvent mixture. The solubility characteristics of the lipid fraction of the meals were correlated with certain of the estimates of biological value. The percentage of the chloroform–methanol-extractable fat which was also extractable with diethyl ether was most significantly correlated with the $S.P.V._{\text{diet efficiency}}$ estimate, probably because $S.P.V._{\text{diet efficiency}}$ is affected by both the balance of available amino acids and the level of available energy in the meals.

Supplementary protein values of the meals after storage showed that the $S.P.V._{\text{weight gain}}$ of the meals which had initially been of above average quality on the basis of this estimate had declined. Meals of poorer initial quality

showed less change upon storage. The amount of available lysine measured in six of the herring meals after storage showed a drop of 25% which lowered the level in each of the stored meals below that in any of the meals in the survey when they were first analyzed.

Growth experiments to determine the primary limiting amino acids in the meals after storage under the conditions for measuring S.P.V. did not generally indicate a deficiency of a single amino acid. Despite the decline in chemically-determined available lysine during storage, the growth response obtained with supplementary lysine was statistically significant only with the White Leghorn chicks and not with the New Hampshire chicks as the test animal.

Supplementation of the fishmeals with a combination of lysine and methionine improved growth in most instances. A response was also noted to a combination of arginine and lysine and to a combination of lysine, arginine and methionine.

The results of the present survey, considered in conjunction with data published by other investigators, indicate that herring meal, as currently produced, is generally of sufficiently high quality to require sensitive biological assays for the detection of variations. Estimates of quality based upon various laboratory analyses for individual amino acids may be useful in detecting meals of distinctly inferior quality, but fail to differentiate among meals of average or better quality. The results of a pepsin-digestibility test of the protein present in chloroform–methanol-extracted meal gave significant correlation with the results of growth response in assays of both gross protein values in which the meal under test is fed to supply 3% of protein at a suboptimal level of dietary protein, and in assays of supplementary protein value in which the meal supplies 8% at an adequate level of protein.

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Seasonal Occurrence and Abundance of Free-Swimming Copepod Nauplii in Narragansett Bay[1]

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ABSTRACT

Night, surface zooplankton samples at one position in the West Passage of Narragansett Bay yielded 10 calanoid, three cyclopoid, and one harpacticoid species of free-swimming copepod nauplii. The seasonal abundance of all species of nauplii combined during the 12 months of study showed significant peaks in spring and mid summer. The holoplankters were grouped into four seasonal categories: *summer–fall*, *winter–spring*, *spring*, and *year-round*; the meroplankters were put in another category. The first two groups dominated the collections. The seasonal occurrence and relative abundance of the individual species of nauplii is shown for the period of study. Included is a short synopsis of the geographical distribution of the adults along the east coast of North America as recorded in the literature.

INTRODUCTION

Few plankton studies along the east coast of North America include nauplii of copepods, although at times they are extremely abundant (e.g. Deevey, 1956). Since nauplii are the youngest active developmental stages and because they are probably more sensitive to the local microenvironment than are the copepodids, it is important that they be included in plankton studies.

Nauplii of *Pseudocalanus minutus* and *Oithona similis* were included in Fish's (1936a, b) studies of the major copepods of the Gulf of Maine and the Bay of Fundy. Conover (1956) gave a detailed account of the ecology and morphology of the nauplii of *Acartia clausi* and *A. tonsa* in Long Island Sound. In the same body of water Deevey (1956) presented evidence of successive generations of all indigenous species of copepods. Most of these same species are found in Narragansett Bay. Frolander (1955) working in Narragansett Bay recorded the seasonal appearance of copepods and estimated the successive generations of locally produced adults. He mentioned collecting nauplii on several occasions.

The methods of collection and enumeration of the nauplii in the West Passage of Narragansett Bay have already been described by Faber (1966). Figure 4 lists the species of copepods collected in this study. The wide annual range of temperature in the West Passage (Fig. 1) permits groups of copepods

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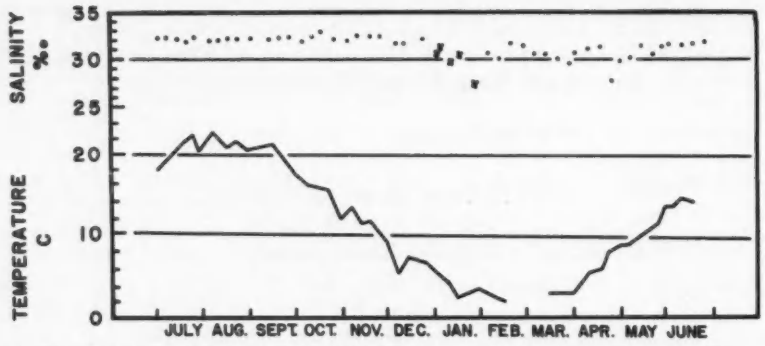

FIG. 1. Surface temperatures and salinities of the sampling station in the West Passage of Narragansett Bay. The temperatures were taken during the period of study, July 1957 to June 1958. Dots indicate salinities measured in 1957 and crosses those in 1958. The salinities from July to December 1957 were taken during the study, but those from February 1957 to June 1957 and January 1958 are presented to show the annual trend of salinity in the West Passage.

with varying temperature tolerances to live and reproduce there. The range of salinity is not very great at that station. Narragansett Bay is unique in that it lies near the southern geographical boundary of several boreal–temperate species of copepods and near the northern boundary of several tropical–temperate species. This account is concerned with the variations in seasonal occurrence and abundance of all identifiable free-swimming copepod nauplii.

SEASONAL ABUNDANCE OF ALL SPECIES OF NAUPLII

The curve showing the numerical abundance of all species of nauplii during the year taken by a No. 12 net in the West Passage has a bimodal appearance (Fig. 2). In this figure daily counts were converted to biweekly means to reduce short-term sampling variations. The significant peaks are in spring and in midsummer with the spring peak attaining 50,000 nauplii/m^3.

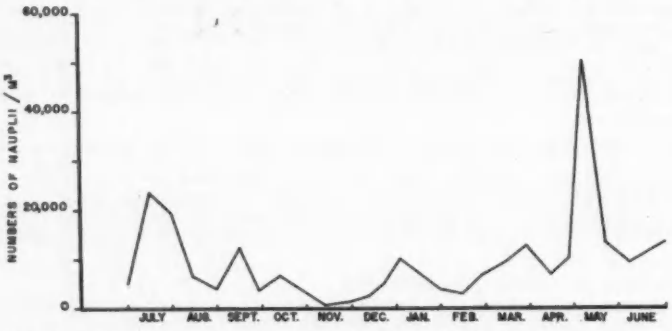

FIG. 2. Numerical abundance of all species of nauplii in the West Passage of Narragansett Bay from July 1957 through June 1958.

The greatest number of nauplii recorded in a single sample was 82,100/m^3 on May 8, of which *Acartia clausi* comprised 69%. On November 18 the fewest number, 548/m^3, was recorded.

Seasonal Occurrence and Relative Abundance of Seasonal Groups of Nauplii

The free-swimming nauplii collected in the West Passage have been grouped into five categories. Four seasonal categories appear logical for the holoplankters, summer–fall, winter–spring, spring, and year-round. The meroplankters have been placed into another category. Each year within the West Passage there is a seasonal appearance of these groups.

Figure 3 shows the seasonal occurrence of the nauplii of these groups in the West Passage with their relative abundance. This figure was constructed

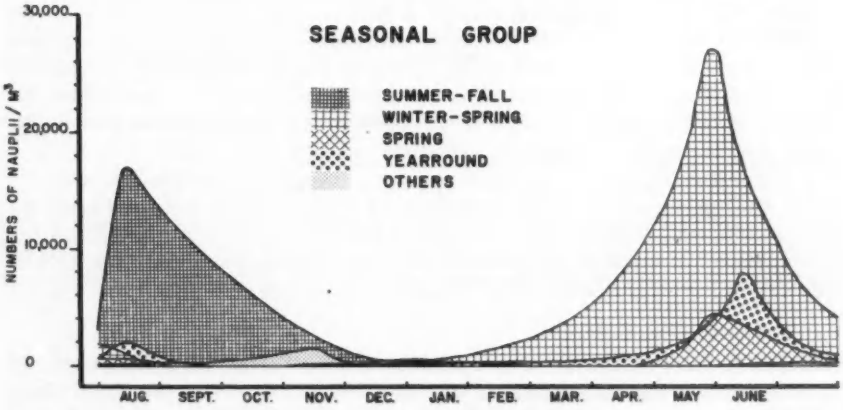

FIG. 3. Seasonal occurrence and relative abundance of the seasonal groups of copepod nauplii in the West Passage, July 1957 through June 1958.

by smoothing by eye the biweekly averages of the members of the various seasonal groups.

Early August was the last of the spring and winter–spring species of nauplii while late June or early July showed the first appearance of the summer–fall nauplii. Apparently temperatures above 16 C were beneficial for hatching and survival of the summer–fall group. These free-swimming nauplii dominated until December.

The other group was continuously present during the summer and fall but not very abundant. The year-round group was absent during late August and most of September.

A drop in the surface water temperature to about 4 C correlated with the appearance of the winter–spring group. November, December, and January were the months of transition which saw the reduction in numbers of the

summer–fall nauplii and the gradual appearance of those of the winter–spring category. The latter group predominated throughout spring. The spring group appeared in mid March but attained their maximum numbers in late April. A week later the winter–spring group attained their maximum numbers. May was the optimum month for the year-round species and this is consonant with their fondness of boreal temperatures.

Seasonal Occurrence and Relative Abundance of Individual Species of Nauplii

The occurrence of any particular copepod species in the West Passage is dependent upon a number of environmental and physiological factors with each species behaving as an individual and not as a member of a temperature-dependent biological group. Deevey (1960) has an excellent discussion on the geographical ranges, temperature limits, and seasonal occurrences of several coastal Atlantic copepods. She states, "it is a common observation that in the northern hemisphere at the northern limits of its range a species appears during summer and fall, and at its southern limits from winter to spring. Where conditions are optimal the year around it should occur throughout the year." Certain groups of copepods, nevertheless, have similar tolerances and these groups can be conveniently discussed together.

The following sections on the 14 species of copepod nauplii collected in the West Passage include a short synopsis of the geographical distribution of the adults along the eastern coast of North America as recorded in the literature and data on the seasonal occurrence and relative numerical abundance of their free-swimming nauplii in the West Passage from July 1957 to June 1958 (Fig. 4).

SUMMER–FALL SPECIES

The summer–fall group of copepods in the West Passage have been reported in American subtropical waters all year long (Grice, 1960), but are found along the New England coast only in the warmest months. *Labidocera aestiva* and *Pseudodiaptomus coronatus* appear to be endemic to the east coast of America while *Acartia tonsa*, *Oithona brevicornis*, and *Paracalanus crassirostris* have been recorded from other oceans (Sewell, 1948). As a group these five species may be considered as tropical–temperate forms.

Acartia tonsa. Along the North American coast *A. tonsa* has been reported from the Gulf of St. Lawrence to the Gulf of Mexico. In the West Passage its nauplii were collected from July into January. They dominated the summer–fall group for their appearance was recorded in numbers greater than $1000/m^3$ from July through October.

Pseudodiaptomus coronatus has the same geographical limits as *A. tonsa* along the North American coast. The nauplii of *P. coronatus* were recorded in the West Passage from July through October with maximum numbers in August.

Labidocera aestiva inhabits the same regions as *A. tonsa* and *P. coronatus* along the North American coast. The nauplii of *L. aestiva* were found in the West Passage from July into November but were never numerically important.

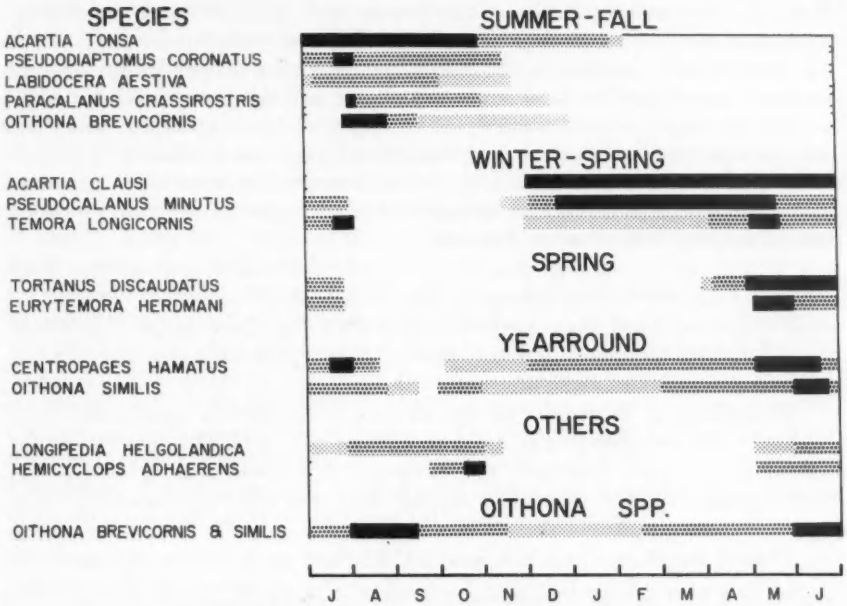

FIG. 4. Seasonal occurrence and relative abundance of individual species of nauplii in the West Passage from July 1957 through June 1958. Small dots represent 1–100 nauplii/m³, large dots 100–1000 nauplii/m³, and solid bars greater than 1000 nauplii/m³. Counts of *O. brevicornis* (C) under *summer–fall* group and *O. similis* (C) under *year-round* group are of copepodites, excluding adults.

Paracalanus crassirostris. The range of *P. crassirostris* along the North American coast occurs from Cape Cod to the Gulf of Mexico. Its nauplii, which were the smallest of any collected in the West Passage, were collected from August into December. Maximum numbers were recorded in early August when they first appeared.

Oithona brevicornis. This small cyclopoid form has the same geographical limits as *P. crassirostris* along the Atlantic coast of North America. Copepodids of *O. brevicornis* were collected in the West Passage from August through December, indicating that the majority of the nauplii of *Oithona* spp. recorded during this time belongs to this species. This assumption suggests that the nauplii of *O. brevicornis* attained numbers greater than 1000/m³ throughout August and into September.

WINTER–SPRING SPECIES

The winter–spring group of copepods is absent from the West Passage only during the warmest period of the year; they predominate in the absence of the summer–fall group. These nauplii first appeared in December and January in contrast to the spring nauplii which appeared later in March and April

(Fig. 4). Although both the winter–spring and spring species are boreal–temperate forms, their geographical ranges differ somewhat.

Pseudocalanus minutus and *Temora longicornis* prefer open waters and can be found year-round in New England's cooler offshore waters. *Acartia clausi* is found in more confined waters and its appearance along the New England coast is restricted in summer by the warm waters and competition with *Acartia tonsa* (Conover, 1956). While *A. clausi* is widespread among cold regions of both th enorthern and southern hemispheres, *T. longicornis* and *P. minutus* are limited to specific boreo-arctic regions.

Acartia clausi. Along the North American coast *A. clausi* has been reported from the Arctic Ocean to Cape Hatteras. In the West Passage its nauplii were collected from November through June. These nauplii dominated the winter–spring period and throughout their appearance were present in numbers greater than 1000/m^3.

Pseudocalanus minutus. In the western Atlantic this species has been collected in the same waters as *A. clausi* and has been recorded from the Arctic Ocean south to Cape Hatteras. The nauplii of *P. minutus* were present in the West Passage from mid November through July and were most abundant from December through May.

Temora longicornis inhabits western Atlantic waters from the southern tip of Greenland to Cape Hatteras. In the West Passage its nauplii were present from late November through late July and were recorded in numbers greater than 1000/m^3 in May and July only.

SPRING SPECIES

The spring group of copepods collected in the West Passage were boreal–temperate species. Their tolerances are apparently similar to the winter–spring group, but they appeared several months later (Fig. 4). Since both species apparently have their southern geographical limits extending further north than the winter–spring species, the later appearance in the West Passage conforms to Deevey's (1960) observations on the relation between the seasonal appearance in Atlantic coastal waters and geographical ranges.

Eurytemora herdmani is an estuarine species which apparently spreads into the West Passage in spring from more brackish waters in Narragansett Bay; *Tortanus discaudatus* prefers higher salinities and more open water. Neither species of nauplii were numerically important.

Tortanus discaudatus. In the western Atlantic *T. discaudatus* has been recorded from the Gulf of St. Lawrence to Delaware Bay. In the West Passage its nauplii were present from late March through July and were recorded in numbers greater than 1000/m^3 in the short period May–June.

Eurytemora herdmani has been found in river mouths from the Gulf of St. Lawrence south to Narragansett Bay. In the West Passage the nauplii of *E. herdmani* were present from May through July. They were recorded in numbers greater than 1000/m^3 in May only.

YEAR-ROUND SPECIES

The year-round group of copepods are strongly eurythermal and euryhaline copepods that have been collected in several oceans (Sewell, 1948). They can be found all year along the New England coast, preferring the more open waters, and can be considered boreal–temperate species.

Centropages hamatus. Along the eastern American coast *C. hamatus* has been recorded from the Strait of Belle Isle to the Gulf of Mexico. Its nauplii were collected throughout the year except for September and the latter part of August. They were recorded in numbers greater than 1000/m^3 in July and during portions of May and June.

Oithona similis. This cyclopoid form is a worldwide species that has been collected locally on the east coast from the Arctic Ocean to Cape Hatteras. It is more oceanic than *O. brevicornis.* Nauplii of *O. similis* were included in the counts of the nauplii of *O. brevicornis.* In order to separate their breeding seasons, copepodids of *O. brevicornis* and *O. similis,* excluding stage VI, were recorded. Copepodids of *O. similis* were recorded in the West Passage year-round except for a short period in late September. Copepodids of *O. similis* in numbers greater than 1000/m^3 were found only in May and June which suggests that the pulse of nauplii recorded in May and June belonged to *O. similis.*

OTHER SPECIES

Hemicyclops adhaerens and *Longipedia helgolandica* are benthonic copepods. Little is known about their ecology or geographical distributions but they appear to be inhabitants of shallow water.

Longipedia helgolandica. Copepodids of *Longipedia* have been collected from Narragansett Bay, Penance Pond at Woods Hole, Martha's Vineyard, Massachusetts (Wilson, 1932), and from Florida and Puerto Rica (Gonzalez and Bowman, 1965). Its adult habitat, according to Wilson, is "rather close to the bottom, where the long second legs assist it in locomotion." Generic identification of my specimens is based on the life history studies of *Longipedia* spp. by Nicholls (1935). Species identification cannot be certain until eggs from ovigerous females are hatched, but Gonzalez and Bowman (1965) claim that all of the *Longipedia* collected in North America are *L. helgolandica* Klie.

Nauplii of *Longipedia* were collected from May through October and into early November. The numbers collected were never very high but indicated successful breeding in the area. The seasonal occurrence of nauplii suggested a preference for surface water temperatures above 10 C and through the summer maximum of 21 C.

Hemicyclops adhaerens. This species appears to be endemic to the eastern North American coast and has only been found at Wickford, Rhode Island, Chesapeake Bay, and Florida (Gooding, 1960). Free-living adult females were found at Wickford in intertidal samples of mud taken under stones.

These nauplii were collected in the West Passage at two distinct periods during the year, late September through October and again during May and June. This unusual distribution of the reproductive periods suggests a strongly

temperature-dependent reaction. A comparison of Fig. 1 and 4 shows that the presence of nauplii was closely associated with surface water temperatures of 10–16 C. The occurrence of nauplii in numbers greater than 1000/m^3 in late October suggests that there is a considerable number of these copepods in Narragansett Bay.

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Selectivity of Gill Nets, Especially to Lake Whitefish[1,2]

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ABSTRACT

This paper re-examines five methods previously described for estimating the selectivity of gill nets as influenced by mesh size, and introduces four more. Those that appeared appropriate for lake whitefish on the basis of preliminary analysis were employed to estimate selectivity using data on whitefish from South Bay, Manitoulin Island, Ontario.

The methods considered most reliable yielded estimates of selectivity curves for whitefish resembling the normal probability function with a positive skew. The length at which the mode occurred was a significantly nonlinear function of mesh size, the variance was approximately proportional to the square of the mesh size, and the coefficient of skewness not related to mesh size.

An implication of these findings is that, for general sampling purposes, standard gangs in which mesh size increased in a certain geometric progression would be more efficient than those with mesh sizes in the usual arithmetic progression. The series for lake whitefish might be $1.40(1.275)^x$ with $x = 0, 1, 2, 3, 4, 5$.

Under the assumption that at peak efficiency all mesh sizes are equally efficient with respect to number of fish, "total efficiency" of a mesh size is defined as the area under the selectivity curve. With respect to number, we estimated that, for whitefish, total efficiency $r = 12 + 5.5$ (mesh size, stretch measure in inches). Here peak efficiency is taken as 100, with length units as inches. Similarly with respect to weight total efficiency $r = 0.80$ (mesh size)$^{3.2}$. Thus with respect to weight, total efficiency increases from about 7.5 for 2-inch mesh to 100 for 4.5-inch mesh to about 200 for 5.5-inch mesh.

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INTRODUCTION

THE PROBABILITY that a fish of a given species and size is caught upon encountering a particular gear of specified construction determines that gear's selectivity toward the species. Though it is possible to estimate absolute probabilities only under certain special conditions, the problem with relative probabilities is more tractable. Reliable estimates of the latter are all that is required for almost all practical purposes.

Most methods of estimating growth and mortality rates require samples representative of the population with respect to size of one or more age groups, or year-classes differing in size. But there is no sampling gear that exhibits equal selectivity towards fish of all sizes even within a particular species. If estimates of selectivity are available, then these may be used to correct estimates of mortality and growth rates based on samples. Alternatively, the knowledge of how selectivity depends on the characteristics of the gear may be used to design a series of gears to yield a sample of known characteristics over a specified size range. A third use is found specifying characteristics of gear for harvesting fish that will permit a realization of certain management objectives, e.g. long-term optimum yield. All this points, of course, to the central role that a knowledge of gear selectivity has in the research and management of fisheries.

We concern ourselves in this paper only with certain aspects of the gillnet selectivity problem. Specifically, we wish to determine how selectivity depends on mesh size when all other characteristics of gillnets are held constant. We restrict consideration almost completely to the problem with lake whitefish, a near ideal species for these purposes. We examined the suitability of various methods given in the literature and derived modifications and new methods. We used the more promising to estimate selectivity curves for lake whitefish in South Bay, Manitoulin Island, Ontario.

Review of the various methods was needed because, for most, the various assumptions had not been spelled out nor the methods clearly defined.

TERMS AND SYMBOLS

The following symbols are used throughout this paper. Reference is always to a particular species and a series of nets differing only in mesh size.

l_j = mean size of fish in size stratum j; sometimes specifically restricted to length, e.g. fork length.

w_j = mean weight of fish in size stratum j.

m_i = size of mesh opening in net i; specifically restricted in the results section to stretch measure.

N_j = either absolute or relative number of fish of size l_j in the population; the population is hypothetical where data are obtained over a long interval or at repeated intervals of time.

$p_j = \frac{1}{N_j}$.

n_{ij} = number of fish of size l_j caught in net i.

π_{ij} = absolute or relative probability that a fish of size l_j will be caught if it encounters mesh m_i.

s_{ij} = selectivity, i.e. relative efficiency, of mesh m_i to fish of size l_j.

S_{ij} = standard selectivity, i.e. $\frac{s_{ij}}{\max_j s_{ij}}$.

L_i = total efficiency, with respect to numbers of fish, of mesh $m_i = \sum_j S_{ij}$.

W_i = total efficiency, with respect to weight of fish, of mesh $m_i = \sum_j S_{ij} w_j$.

Type A selectivity curve is fitted to points $\hat{s}_{ij}$ or $\hat{S}_{ij}$ on l_j for fixed m_i.

Type B selectivity curve is fitted to points $\hat{s}_{ij}$ or $\hat{S}_{ij}$ on m_i for fixed l_j. (This type used on occasion as an intermediate step in estimating Type A curves.)

SOME METHODS OF ESTIMATING GILLNET SELECTIVITY

We may, for convenience in discussion, distinguish between three different general methods of determining how selectivity is influenced by mesh size. These are here denoted as the direct, indirect, and iterative methods.

The direct method requires a knowledge of the size composition of the population and then estimates selectivity simply by relating the composition of the sample to that in the population.

The indirect method requires certain mathematical assumptions about the selectivity curve, but no knowledge of the population composition. It estimates how s_{ij} depends on m_i for fixed l_j and then uses these estimates to infer how s_{ij} depends on l_j for fixed m_i.

The interative method also requires certain mathematical assumptions. On the basis of successive iterations on $\hat{N}_{ij}$ it yields a scatter of points considered, according to some criterion, to be satisfactory for fitting a selectivity curve.

In all of these methods we have assumed that no "gear saturation" occurred—that the number of fish already entangled in the net in no way influenced subsequent behavior of other fish and the net. Also we assumed that no "spill-over" occurred—that large fish did not lead along the series until they encountered a large enough mesh in which perhaps to become entangled. The sampling design was such as to minimize both of these tendencies, even if present: the whitefish populations were not abundant during the period from

which the data derive; gill nets were set only 1 night at a time; and the nets were hung with gaps between different mesh sizes. Further, we take the net manufacturers' specifications as though they were completely accurate; periodic measurements of mesh sizes indicated that they were approximately as stated.

Various more specific methods are described below under these three general headings.

I. Direct Method

The direct approach is used where the size frequency distribution of the population vulnerable to the gear is either known or reliably estimated by other methods. The steps are:

(i) Given N_j's or $\hat{N}_j$'s, then

$$\tilde{s}_{ij} = \frac{n_{ij}}{N_j} \text{ or } \frac{n_{ij}}{\hat{N}_j}$$

(ii) Plot $\tilde{s}_{ij}$ vs. l_j for each net i and draw a smooth curve or fit a likely mathematical model to the points for each i.

(iii) Determine $\hat{s}_{ij}$ from the curve or mathematical expression.

(iv) Calculate $\hat{S}_{ij} = \dfrac{\hat{s}_{ij}}{\max\limits_{j} \hat{s}_{ij}}$

This method has two great advantages over the other two general methods, i.e. no mathematical assumptions are required, and data from only one mesh size are needed. On the other hand, the requirement that the population size composition be known has the practical implication that the data came from a short period of time. Further, the population must either be sampled during the same period with a gear of known selectivity, or a known population (e.g. of tagged fish) must be released into the environment at the start of the sampling.

II. Indirect Methods

These methods do not require estimates or iterations on the N_{ij}. Data must consist of catches by size strata of a series of different mesh sizes. The logic of these methods derive from the assumption that all fish of a given length stratum are equally likely to encounter all nets. Depending on the specific method, Type A curves or Type B curves both may be estimated. It is convenient to consider first those methods that estimate Type A curves utilizing further assumptions.

A. Type A Curves

To estimate Type A curves by indirect methods without recourse to Type B curves, we must assume a mathematical model for the Type A selectivity

curve. The literature suggests a smooth unimodal curve with arms descending to zero to be suitable for streamlined fish without spines, hooks, teeth, or projecting opercular bones to catch on the net, i.e. for those fish that invariably are caught wedged into the mesh. For those species likely to be caught in a variety of ways, Holt (1963) has suggested maintaining separate statistics and estimating selection curves for each capture location, and then combining these in some manner to obtain an overall selection curve. We will restrict discussion to the simple case.

Preliminary analysis of the data (e.g. via Type B curves or one of the iterative methods outlined below) may suggest an appropriate model for the Type A curves. Three likely models are given below and the steps necessary for estimating the respective parameters of each are outlined.

1. *Normal model.* Holt (1963) proposed this approach in 1957. We review first Holt's special case and then suggest a more general model.

Assumptions and steps in the solution are as follows:

(i) Assume that

$$s_{ij} = \frac{k_1}{\sigma} e^{-(l_j - \bar{l}_i)^2/2\sigma^2},$$

and that $\bar{l}_i = k_2 m_i$ where $\bar{l}_i$ is the mean of the Type A selectivity curve of net i;

σ^2 is the variance, constant over all i;

k_1 and k_2 are coefficients, constant over all i.

(ii) Consider s_{ij} and $s_{i+1,j}$, where $i+1$ denotes the net of next larger mesh to that of net i.

$$\text{Since } \frac{s_{i+1,j}}{s_{ij}} = \frac{n_{i+1,j}/N_j}{n_{ij}/N_j} = \frac{n_{i+1,j}}{n_{ij}} = R_{i+1,i,j}$$

calculate the ratios $R_{i+1,i,j}$, where

$$R_{i+1,i,j} = \frac{\frac{k}{\sigma} e^{-(l_j - \bar{l}_{i+1})^2/2\sigma^2}}{\frac{k}{\sigma} e^{-(l_j - \bar{l}_i)^2/2\sigma^2}}$$

$$= e^{-\frac{1}{2\sigma^2}\left[2(\bar{l}_i - \bar{l}_{i+1}) l_j + \bar{l}_{i+1}^2 - \bar{l}_i^2\right]}.$$

(iii) Now, $ln R_{i+1,i,j} = \frac{1}{2\sigma^2}(\bar{l}_i^2 - \bar{l}_{i+1}^2) + \frac{1}{\sigma^2}(\bar{l}_{i+1} - \bar{l}_i) l_j$ is a linear function in l_j:

$$Y_j = a + bl_j.$$

Estimate a and b by linear regression methods.

(iv) Further, $\frac{\hat{a}}{\hat{b}} = -\frac{1}{2}(\hat{l}_i + \hat{l}_{i+1}) = -\frac{\hat{k}_2}{2}(m_i + m_{i+1})$

and therefore $\hat{k}_2 = -\frac{2\hat{a}}{\hat{b}(m_i + m_{i+1})}$.

Solve for $\hat{k}_2$, then

$$\hat{l}_i = \hat{k}_2 m_i$$

and finally

$$\hat{\sigma}^2 = \frac{\hat{l}_{i+1} - \hat{l}_i}{\hat{b}}.$$

(v) The selectivity curves for nets i and $i + 1$ are obtained by substituting $\hat{\sigma}^2$, $\hat{l}_j$, and $\hat{l}_{i+1}$ in the equation

$$S_{ij} = e^{-\frac{1}{2\sigma^2}(l_j - \bar{l}_i)^2}.$$

The special case with σ constant over i may seldom be a suitable model. Though Holt (1963) found it satisfactory in a number of instances, various workers have shown that it was violated by their data. A more likely assumption is that the coefficient of variation, $\frac{\sigma}{\bar{l}}$, is constant and an assumption of this general sort is implicit in some other approaches (see below).

Assumptions and steps in the solution are as follows:

(i) Assume that

$$s_{ij} = \frac{k_1}{\sigma_i} e^{-(l_j - \bar{l}_i)^2/2\sigma_i^2}.$$

(ii) Calculate ratios and take logarithms as before:

$$ln R_{i+1,i,j} = \left[ln\left(\frac{\sigma_i}{\sigma_{i+1}}\right) + \frac{\bar{l}_i^2}{2\sigma_i^2} - \frac{\bar{l}_{i+1}^2}{2\sigma_{i+1}^2}\right] + \left(\frac{\bar{l}_{i+1}}{\sigma_{i+1}^2} - \frac{\bar{l}_i}{\sigma_i^2}\right) l_j + \left(\frac{1}{2\sigma_i^2} - \frac{1}{2\sigma_{i+1}^2}\right) l_j^2.$$

This function has the form

$$Y_j = a + bl_j + cl_j^2.$$

Estimate a, b, and c by multiple regression methods.

(iii) Assume tentatively that $\sigma_i = k_{i+1,i}m_i$ and $\sigma_{i+1} = k_{i+1,i}m_{i+1}$.

(We will estimate a $k_{i+1,i}$ for each set of ratios obtained as in (ii) above.)

(iv) Solve for $\bar{k}$ where

$$\bar{k} = \sqrt{\frac{1}{2\hat{c}}\left(\frac{1}{m_i^2} - \frac{1}{m_{i+1}^2}\right)}$$

(v) Solve for $\tilde{\sigma}_i$ and $\tilde{\sigma}_{i+1}$ using the relationship

$$\tilde{\sigma}_i = \bar{k}_{i+1,i}m_i \text{ and } \tilde{\sigma}_{i+1} = \bar{k}_{i+1,i}m_i$$

(vi) Solve for $\bar{\bar{l}}$ using the function

$$\bar{\bar{l}}_i = \frac{\frac{\tilde{\sigma}_{i+1}^2}{\tilde{\sigma}_i^2}\left[2\hat{b} \pm \sqrt{\frac{7\hat{b}^2\tilde{\sigma}_{i+1}^2}{2} + ln\left(\frac{\tilde{\sigma}_i}{\tilde{\sigma}_{i+1}}\right) - \hat{a}}\right]}{ln\left(\frac{\tilde{\sigma}_i}{\tilde{\sigma}_{i+1}}\right) - \frac{\hat{b}^2\tilde{\sigma}_{i+1}^2}{2} - \hat{a}}$$

and for $\bar{\bar{l}}_{i+1} = \tilde{\sigma}_{i+1}^2\left(\hat{b} + \frac{\bar{\bar{l}}_i}{\tilde{\sigma}_i^2}\right)$.

(vii) Repeat the above procedure for net combinations 1 and 2, 2 and 3, 3 and 4, . . . , $i-1$ and i, i and $i+1$, etc. In this manner two estimates of each $\bar{\bar{l}}_i$ and σ_i are obtained except for the smallest and largest mesh sizes.

(viii) By curvilinear regression methods estimate the functional relationships between the $\bar{\bar{l}}_i$ and m_i and $\tilde{\sigma}_i$ and m_i. From these estimated relationships determine final estimates, $\hat{l}_i$ and $\hat{\sigma}_i$, for any m_i of interest.

(ix) The final estimates are then substituted into the relationship

$$\hat{S}_{ij} = e^{-\frac{1}{\hat{\sigma}_i^2}(l_j - \hat{l}_i)^2},$$

which may be evaluated at any l_j for any m_i.

The above method first assumes that the standard deviation is proportional to mesh size and then uses net combinations and a final pooling of data in curvilinear regression to minimize errors in the estimates due to this assumption. (This general approach is also used with the next two models.) Our unsuccessful attempts to use the general normal model with lake whitefish data suggested

this model was quite sensitive to inadequacies of the data, or deviations from assumptions, or both.

2. *Olsen exponential model.* Olsen (1959) used an exponential model suggested by Holt (1963) and bearing some resemblance to the normal. Assumptions and steps in obtaining estimates are as follows:

(i) Assume that

$$s_{ij} = k_1 e^{-f(l)}, \text{ where } k_1 \text{ is a constant.}$$

(ii) Assume that $\bar{l}_i = k_2 m_i$, where k_2 is a constant.

(iii) Compute ratios $R_{i+1,i,j}$ for nets i and $i+1$ as before.

(iv) Estimate the functional relationship of $ln\ R_{i+1,i,j}$ on l_j by curvilinear regression. If the functional relationship is parabolic (i.e. second order) choose the following model for $f(l)$:

$$f(l) = u(l_j - \bar{l}_i)^3 + v(l_j - \bar{l}_i)^2.$$

(v) Then

$$ln R_{i+1,i,j} = [\bar{l}_{i+1} - \bar{l}_i]\ [u(\bar{l}_{i+1}^2 + \bar{l}_{i+1}\bar{l}_i + \bar{l}_i^2) - v(l_{i+1} + l_i)] + [\bar{l}_{i+1} - \bar{l}_i]\ [3u(l_{i+1} + l_i) - 2v]\ l_j + [3u(\bar{l}_{i+1} - \bar{l}_i)]\ l_j^2.$$

This function is of the form

$$Y_j = a + bl_j + cl_j^2$$

and a, b, and c are estimated by curvilinear regression methods.

(vi) Solve for $\hat{v}$, $\hat{k}_2$ and $\hat{u}$ where

$$\hat{v} = \frac{1}{24\hat{a}(m_{i+1} - m_i)}\left[-3(m_{i+1} + m_i)\ (\hat{b}^2 - 4\hat{a}\hat{c}) \pm \hat{b}\sqrt{(9\hat{b}^2 - 24\hat{a}\hat{c})\ (m_{i+1} + m_i)^2 - 48\hat{a}\hat{c}m_i m_{i+1}}\right],$$

$$\hat{k}_2 = \frac{\hat{b}}{2\hat{v}(m_{i+1} - m_i) - \hat{c}(m_{i+1} + m_i)},$$

and $\hat{u} = \dfrac{\hat{c}}{3\hat{k}_2\ (m_{i+1} - m_i)}$.

(vii) Olsen had catch data from three nets and obtained three estimates of each of $\hat{k}$, $\hat{u}$, and $\hat{v}$, using ratios of net combinations 1 and 2, 2 and 3, and 1 and 3. He calculated simple means of the three estimates for final estimates and solved for the $\bar{l}_i$ using the relationship $\bar{l}_i = \hat{k}_2 m_i$.

(viii) Final estimates of u, v, and l_i are then substituted in the function

$$S_{ij} = e^{-u(l_j - \bar{l}_i)^2 - v(l_j - \bar{l}_i)^3},$$

which may be evaluated at any mesh size and fish size.

(vii′) As an alternative to (vii) above, especially if data from more than three nets are available, consider $k_2 = k_{i+1,i}$ as a first approximation. Proceed as with the normal model to obtain two estimates of each k, u, and v for all nets except those with smallest and largest mesh. Estimate the functional relationship of each k, u, and v to m_i using curvilinear regression and obtain final estimates from the relationship. Then proceed as in (vii) above.

A theoretical difficulty with Olsen's model is that the right desending arm approaches but never reaches zero. Instead it eventually rises steeply to infinity. It cannot be used as a probability distribution and does not have finite moments. Olsen's reference to a "mean" is really to the location of the peak in the first mode. These difficulties may have practical significance, as is shown with lake whitefish data below.

3. *Gamma model.* The gamma distribution can have a variety of shapes. As with the normal, the gamma model is a probability distribution and both arms fall to zero. Assumptions and steps follow:

(i) Assume that

$$s_{ij} = \frac{1}{\Gamma(\alpha_i + 1)\beta_i^{\alpha_i + 1}} l_j^{\alpha_i} e^{-l_j/\beta_i}.$$

(ii) Compute ratios and take logarithms as with previous models.

$$ln\left(R_{i+1,i,j}\right) = ln\left(\frac{n_{i+1,i,j}}{n_{ij}}\right) = ln\left[\frac{\Gamma(\alpha_i + 1)\beta_i^{\alpha_i+1}}{\Gamma(\alpha_{i+1} + 1)\beta_{i+1}^{\alpha_{i+1}+1}}\right] + \left(\frac{1}{\beta_i} - \frac{1}{\beta_{i+1}}\right) l_j + (\alpha_{i+1} - \alpha_i)\, lnl_j.$$

This equation is of the form

$$Y_j = a + bl_j + clnl_j.$$

(iii) Estimate a, b, and c by regression methods.

(iv) The mode of the gamma distribution occurs at

$$l = \alpha\beta.$$

Tentatively assume that

$$\alpha_i\beta_i = k_{i+1,i}m_i \text{ and}$$

$$\alpha_{i+1}\beta_{i+1} = k_{i+1,i}m_i.$$

The solution for α_i, α_{i+1}, β_i, β_{i+1}, and $k_{i+1,i}$ is iterative, as follows.

(v) From the data obtain a first estimate of $k_{i+1,i} = \tilde{k}$ as follows:

Determine $\bar{l}_i = l_{ij}$ at $\max_i (n_{ij})$.

Compute $\tilde{k} = \dfrac{\sum_i \bar{l}_i}{\sum_i m_i}$.

(vi) Obtain first estimates of the α's and β's using $\tilde{k}$:

$$\tilde{\alpha}_i = \frac{m_i}{m_i - m_{i+1}} (\tilde{k}\hat{b}m_{i+1} + \hat{c}).$$

$$\tilde{\alpha}_{i+1} = \hat{c} + \tilde{\alpha}_i.$$

$$\tilde{\beta} = \frac{\tilde{k}m_i}{\tilde{\alpha}_i}.$$

$$\tilde{\beta}_{i+1} = \frac{\tilde{k}m_{i+1}}{\tilde{\alpha}_{i+1}}.$$

Compute $\tilde{c} = ln\left[\dfrac{\Gamma(\tilde{\alpha}_i + 1)\tilde{\beta}_i^{\alpha_i+1}}{\Gamma(\tilde{\alpha}_{i+1} + 1)\tilde{\beta}_{i+1}^{\tilde{\alpha}_{i+1}+1}}\right]$.

(vii) Compute $(\tilde{c} - \hat{c})^2$.

(viii) Systematically change $k_{i+1,i}$, estimate $\tilde{c}$ until the $k_{i+1,i}$ is found which minimizes $(\tilde{c} - \hat{c})^2$. Estimates of both α's and both β's are thus available.

(ix) Repeat the above steps with data from nets number 1 and 2, 2 and 3, 3 and 4, etc. Each comparison yields estimates of the corresponding α's and β's.

(x) As with previous models, calculate curvilinear regressions of $\tilde{\alpha}_i$ and of $\tilde{\beta}_i$ on m_i and obtain final estimates, $\hat{\alpha}_i$ and $\hat{\beta}_i$, from these relationships.

(xi) Substitute final estimates into the relationship

$$\hat{S}_{ij} = \left(\frac{l_j e}{\hat{\alpha}_i \hat{\beta}_i}\right)^{\hat{\alpha}_i} e^{-\frac{l_j}{\hat{\beta}_i}}$$

to obtain a standard Type A curve. (This formula utilized Sterling's formula to ease computations.)

As with the general normal model, the gamma model did not yield unique estimates for lake whitefish, perhaps for the same reasons. If we stop with the first estimate of $k_{i+1,i} = \bar{k}$ and delete steps (vii) to (x) we can at least get an idea of the shape of the selectivity curve and how it compares with those of other methods. Using this approach with the data on which Olsen based his A curve (his fig. 2) showed very close agreement between his result and ours except in the mid-left arm where a discrepancy of about 0.12 (12%) occurred. Results with lake whitefish using this shorter method are discussed further below.

B. TYPE B CURVES

Estimating Type B curves involves essentially plotting histograms of n_{ij} by m_i for fixed l_j, transforming the m_i for the various l_j according to some assumed function $f(m_i, l_j)$ so that all histograms approximate one curve. The curve is then fitted by eye, or statistically to a likely mathematical model.

The methods described below become quite messy unless the data are from a series of nets in which mesh sizes increase from small to large in some mathematically fixed manner. (Otherwise the histograms have bars of variable width and the task of curve fitting becomes more complicated.) The following examples illustrate satisfactory series:

m_i when	$i = 1$	$i = 2$	$i = 3$	$i = 4$	$i = 5$
$1.00 + 0.5i$	1.50	2.00	2.50	3.00	3.50
$(1.50)^i$	1.50	2.25	3.37	5.06	7.60
$3.35(6 - i)^{-\frac{1}{2}}$	1.50	1.68	1.937	2.37	3.35

If the mesh sizes are not in a linear series, the first step is to transform them, if possible, to a linear series. Then if all nets have equal overall dimensions, and if a fixed proportion of the catch in each net is sampled,

$$\frac{n_{ij}}{\sum_i n_{ij}} = \hat{\pi}_{ij}.$$

Thus a plot of n_{ij} vs. (transformed) m_i yields an estimate of the Type B curve at size l_j.

The following three methods require (ideally) an experimental design as outlined above, but further assumptions differ.

1. *Graphical method of McCombie and Fry.* McCombie and Fry (1960) proposed and used essentially this method. Not all their nets were in a simple arithmetic series and consequently they resorted to iterations somewhat similar to those of Ishida (see below). We will not refer to these difficulties further here, but simply assume a linear series. Assumption and steps follow.

(i) Assume all s_{ij} are equal for those combinations of i and j for which $\frac{m_i}{l_j}$ are equal. Alternatively stated, $m = k(a,s)l$ where a denotes the "arm" of the selectivity curve, either ascending or descending, and s the selectivity value to which k has reference. Figure 1 illustrates this assumption.

(ii) The Type B selectivity curve at size l_j, satisfying the above assumption, is estimated by $\hat{\pi}_{ij}|_{l_j}$ provided we set $\hat{\pi}_{ij} = s_{ij}$ at $l_j = l$.

(iii) All the $\hat{\pi}_{ij}|_{l_j}$ may now be transposed in their individual planes $m = k(a,s)l$ to fall on a single plane at either $l = l'$ or $m = m'$. The former case

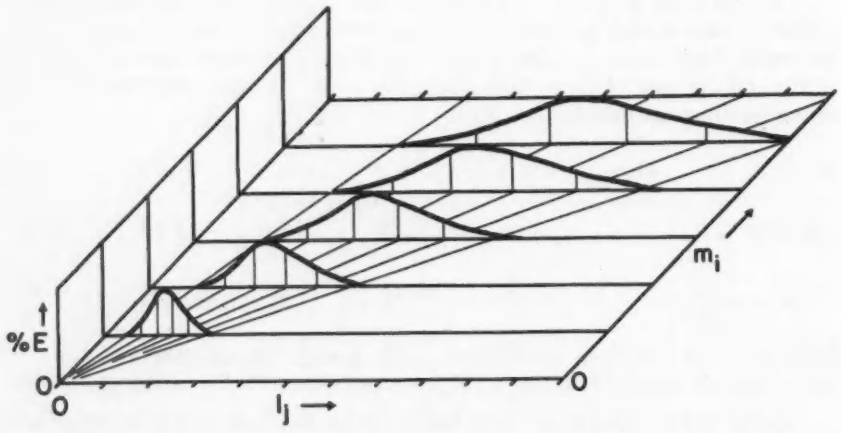

FIG. 1. Graphic representation of an assumption common to the methods used by McCombie and Fry (1960), Ishida (1962, 1964), and Gulland and Harding (1961).

would yield a common scattergram for a Type B curve at l', the latter a scattergram for a Type A curve at m'. In the latter case, the transposition is accomplished by relocating $\hat{\pi}_{ij}l_j$ from (m_i,l_j) to (m',l_{ij}) where m' is arbitrary and constant over all i and j, and $l'_{ij} = \frac{m'l_j}{m_i}$. Having "mapped" all the $\hat{\pi}_{ij}l_j$ into $m = m'$, a curve is fitted to the points by eye, or by using a suitable mathematical model and objective estimation methods.

(iv) Estimates of Type A curves at any mesh size, say m_1, may then be derived from the composite estimate by mapping a series of $\hat{s}$, spanning the range of $\hat{s}$ in $m = m'$, from their respective (m',l') to $\left(m_1, l = \frac{m_1,l'}{m'}\right)$.

If the Type B curves turn out to be very similar to normal probability curves, then (i) above is equivalent to assuming that the coefficient of variation, $\frac{\sigma_j}{l_j}$, is constant over j. Sample distributions of biological measurements often exhibit this characteristic.

McCombie and Fry considered girth of whitefish to be the best measure to use as l_j, on the assumption that girth is the major factor affecting capture probability. But the swimming thrust that the fish can exert may be more important and this thrust may be more closely correlated with length than with girth.

Though these authors used girth as a measure of l_j, it was obtained by transforming length measurements according to an estimated linear girth–length relationship since they had girth measurements for relatively few of the fish sampled. Thus their effective assumption corresponding to (i) was that all $\hat{s}_{ij}$ are equal for those combinations of i and j for which $\frac{m_i}{l_j - a}$ are equal, where l_j is length of fish, and a is fixed by the girth–length relationship. We present evidence below that this assumption is approximately correct for only a limited range of m_i and l_j with lake whitefish.

McCombie and Fry found that a logarithmic transformation of $\frac{l_j - a}{m_i}$ yielded approximately symmetric curves with lake whitefish. Use of $\frac{m_i}{l_j - a}$ untransformed also yields approximately symmetric curves.

A somewhat more realistic approach than to fix a for all combinations of i and j would be to estimate iteratively a series of different a's for different sets of l_j.

2. *Graphical method, "variance" constant.* The approach is similar to previous one, but with a different basic assumption and that limited to relatively short ranges of l_j. Steps are:

(i) Assume that for fixed j, within a specified range of l_j,

$$m = k(a,s) + k_1 l + k_2 l^2 + \ldots + k_r l^r$$

where r may be 3, 4, 5, . . . etc.

$$\hat{\bar{m}}_j = \frac{\sum_i m_i n_{ij}}{\sum_i n_{ij}},$$

that b is constant for all combinations of i and j, and that all s_{ij} are equal for those combinations of i and j for which $\frac{\bar{m}_j - a}{l_j}$ are equal holding a constant. If the Type B curve turns out to be normal, this assumption states that variance is constant within the set l_j.

(ii) For each set of l_j's, b is estimated as follows. For each j stratum, calculate $\tilde{\bar{m}}_i = \frac{\sum_i n_{ij} m_i}{\sum_i n_{ij}}$. Fit a line (by regression or by eye) to the plot of $\tilde{\bar{m}}_i$ vs. l_j. The slope of this line defines the $\hat{b}$ for that set.

(iii) For each $\bar{\pi}_{ij}$ in the set l_j calculate a corresponding $m_i' = m_i - b(l_j - \bar{l}_j)$. (This can be done graphically with parallel rules.)

(iv) Plot $\bar{\pi}_{ij}$ vs. m_i' and draw a curve to the scatter of points with the restriction that the area under the curve be unity, or some other constant, for all l_j sets. The resulting Type B curve corresponds to the $\bar{l}_j$ of a particular set.

(v) The ordinates, $\bar{\pi}_{ij}$, of each Type B curve are now multiplied by the factor $\frac{d}{\max_i (\bar{\pi}_{ij})}$, where $\max_i(\bar{\pi}_{ij})$ is the ordinate at the mode of the curve and d is an arbitrary constant over all l_j sets. This adjusts each Type B curve to agree with the assumption that at peak efficiency nets of different mesh are all equally efficient.

(vi) Finally, Type A curves are obtained by reading $\hat{s}_{ij}$ at various $\bar{l}_j$ and m_i from Type B curves and plotting the $\hat{s}_{ij}$ at corresponding $\bar{l}_j$ for fixed m_i.

If the Type B curves turn out to be normal, then (i) above implies that variance, σ^2, is constant within a set of l_j. However, restricting the set to a short range in l_j, and drawing a mean curve to apply at $\bar{l}_j$, tends to reduce error if the assumption is inaccurate.

This method yielded more reliable estimates for lake whitefish at both the lower and upper extremes of l_j than did the previous method.

3. *Computational method, skew-normal model.* The approach here is to assume a mathematical model for the Type B curve and to obtain best fit by calculating the moments of the distribution in each size stratum. Such models might be the normal, log-normal, skew-normal, gamma, some of the Pearson curves, etc. Here a skew-normal model is assumed. Steps are as follows:

(i) Assume

$$s_{ij} = \frac{1}{\sqrt{2\pi}\,\sigma_j} e^{\frac{-(m_i-\bar{m}_j)^2}{2\sigma_j^2}} \left\{1 - \frac{1}{2} q_j \sigma_j^{\frac{3}{2}} \left[\frac{m_i - \bar{m}_j}{\sigma_j} - \frac{(m_i-\bar{m}_j)^3}{3\sigma_j^3}\right]\right\}$$

This is the normal probability distribution corrected for skewness using the first two terms in a Gram-Charlier series (Croxton and Cowden, 1939).

(ii) For each l_j calculate $\tilde{\bar{m}}_j = \dfrac{\sum_i n_{ij} m_i}{\sum_i n_{ij}}$.

(iii) By multiple regression methods, estimate the relationship of $\tilde{\bar{m}}_j$ to l_j and from it read a corrected estimate of $\bar{m}_j$ for each l_j.

(iv) For each j estimate the variance, $\tilde{\sigma}_j^2 = \dfrac{\sum_i n_{ij}(m_i - \hat{\bar{m}}_j)^2}{\sum_i n_{ij}}$.

(v) By curvilinear regression estimate the relationship of $\tilde{\sigma}_j^2$ to l_j and obtain final estimates, $\hat{\sigma}_j^2$, from this relationship.

(vi) For each j estimate the coefficient of skewness:

$$\tilde{q}_j = \frac{\sum_i n_{ij}(m_i - \hat{\bar{m}}_j)^3}{\sum_i n_{ij}}.$$

(vii) By curvilinear regression methods determine the relationship of $\tilde{q}_j$ on l_j and obtain final estimates, $\hat{q}_j$, from this relationship.

(viii) The estimates, $\hat{\bar{m}}_j$, $\hat{\sigma}_j^2$, and $\hat{q}_j$, are then inserted into the model for any desired j stratum to obtain the Type B curve for size l_j fish.

(ix) Each Type B curve is then standardized and Type A curves estimated as in (v) and (vi) of the preceding method.

We had this method programmed for an electronic computer and used it to obtain what we believe to be more reliable results than from any of the other methods.

III. Iterative Methods

Essentially these methods arrive at estimates by making assumptions about the relationship of s_{ij} to m_i and l_j, then iterating with respect to the N_j to yield a "satisfactory" scatter of points to which a curve is fitted.

1. ISHIDA'S METHOD

An outline and some applications of this method may be found in Ishida (1962, 1964). Assumptions and steps follow:

(i) Again, assume all s_{ij} are equal for those combinations of i and j for which $\frac{l_j}{m_i}$ are equal.

(ii) Assign a particular set of preliminary values to the $p_j = \tilde{p}_j$. (A first choice might be to set each $\tilde{p}_j = 1$.) Calculate $\tilde{s}_{ij} = \tilde{p}_j n_{ij}$.

(iii) Calculate $\frac{l_j}{m_i}$ for each n_{ij} and determine $\max(c) = \max_{i,j}\left(\frac{l_j}{m_i}\right)$ for which $n_{ij} \neq 0$, and $\min(c) = \min_{i,j}\left(\frac{l_j}{m_i}\right)$ for which $n_{ij} \neq 0$.

(iv) Choose a particular $m_i = m'$ onto which to "project" all data between $\max(c)$ and $\min(c)$, including those for which $n_{ij} = 0$. Calculate $Y_{ij} = \frac{l_j m'}{m_i}$ for each n_{ij}, where Y_{ij} indicates the point on the line $m = m'$ where the corresponding $n_{ij}\tilde{p}_j$ falls.

(v) Order all Y_{ij} from largest to smallest denoting the ordered terms $(Y_{ij})_1, (Y_{ij})_2, \ldots,$ and the corresponding as $(n_{ij}\tilde{p}_j)_1, (n_{ij}\tilde{p}_j)_2, \ldots$.

(vi) Determine $\max(j)$ and $\min(j)$ from the array. Certain p_j's will not be estimable, i.e. those for which no n_{ij}'s were observed. Identify these j's where $\max(j) < j < \min(j)$ for which all $n_{ij} = 0$ and assign to each of the corresponding p_j's an arbitrary value, e.g. 1.

(vii) Fit a tentative (Type A) curve to the data. From inspection of the relative locations of points in the scatter corresponding to the various p_j's, estimate new p_j's, replot the points, fit another curve, etc. Continue iterating on p_j's until a "satisfactory" scatter of points is achieved on which is based the relative selectivity curve for mesh size m'. The selectivity curves for other mesh sizes are obtained by applying assumption (i) to these estimates.

We have used quotes on the term "satisfactory" for two reasons; Ishida did not state an objective criterion by which to judge goodness of fit, and secondly we doubt that an objective criterion exists which, if applied, would yield unique estimates of all the p_j's.

We used "minimum sum of squares of successive differences" as an objective criterion. Details follow.

The sum of squares of successive differences, SSSD, is defined as

$$f(p_{\max(j)}, \ldots, p_{\min(j)}) = [(p_j n_{ij})_1 - 0]^2 + [(p_j n_{ij})_2 - (p_j n_{ij})_1]^2 + [(p_j n_{ij})_3 - (p_j n_{ij})_2]^2 + \ldots .$$

The SSSD is minimized when

$\frac{\delta f}{\delta p_j} = 0$ for each j. Each expression for $\frac{\delta f}{\delta p_j}$ is linear in p_j and if this set of normal equations can be solved for the p_j's then there would be a unique best scatter of points.

We examined this analytic method using data from table 2 of Ishida (1964). We lumped length strata to obtain data in 3 mesh sizes in 5 length strata and found no solution for the p_j's. Similarly, a computer program using all the data in Ishida's table 2 yielded no solution. We conclude that this (analytic) method does not in general lead to a solution of the p_j's. (There may be special cases in which it would do so.)

Our failure to obtain a unique solution implies that the final outcome of iterations may be influenced by the way iterations are begun, by a preconceived notion of the shape of a selectively curve, by the criteria applied, etc.

2. GULLAND AND HARDING'S METHOD

Gulland and Harding (1961) used this method after they found some of the simpler methods (those of Holt, McCombie and Fry, above) unsuitable. Essentially it combines aspects of the McCombie and Fry and the Ishida methods. Assumptions and steps follow.

(i) Assume all s_{ij} are equal for those combinations of i and j for which $\frac{m_j}{al_j + b}$ are equal, where a and b are constant over all i and j.

(ii) To estimate a and b, plot n_{ij} vs. m_i for fixed l_j, fit a smooth curve, locate $\tilde{M}_j = m_i$ corresponding to the peak of the curve, plot all $\tilde{M}_j$ vs. l_j and estimate a and b by linear regression methods. Let $\hat{M} = \hat{a}l_j + \hat{b}$.

(iii) Now determine $\tilde{\pi}_{ij} = \frac{n_{ij}}{\max_j(n_{ij})}$ from the plots of n_{ij} vs. m_i.

(iv) Plot all $\tilde{\pi}_{ij}$ vs. corresponding $\log \frac{\hat{M}_j}{m_i}$ and obtain a first estimate of $s_{ij} = \tilde{s}_{ij}$.

(v) Now $\tilde{N}_j = \frac{n_{ij}}{\tilde{s}_{ij}}$, or pooling over all i,

$$\tilde{\tilde{N}}_j = \frac{\Sigma n_{ij}}{\Sigma \tilde{s}_{ij}}.$$

(vi) Finally iterate as follows. Calculate $\tilde{\tilde{s}}_{ij} = \frac{n_{ij}}{\tilde{\tilde{N}}_j}$ and plot all $\tilde{\tilde{s}}_{ij}$ vs. $\log \frac{\hat{M}_j}{m_i}$. Draw a smooth curve and obtain further corrected estimates of s_{ij} and N_i. Continue iterating until iterations have converged satisfactorily and obtain final estimates of s_{ij} and N_j.

As with Ishida's method, the ultimate criterion here is a subjective one. To what extent the estimate can be influenced by subjectivity is not known.

The above completes our survey of some likely methods that might be applied in estimating gillnet mesh selectivity to lake whitefish. We used all approaches except that of Gulland and Harding and outline some further details and results below.

RESULTS WITH LAKE WHITEFISH DATA

We provide results in the same sequence as the survey of methods. Some of the details of estimation are also included. In each case we graph the estimated selectivity of $4\frac{1}{2}$-inch stretch measure nylon gillnet toward lake whitefish and compare the result with what we consider to be the most reliable estimate, that derived using the computational method with the skew-normal model.

With the exception of those used in the direct method, all data were obtained from lake whitefish, *Coregonus clupeaformis*, in South Bay, Manitoulin Island, Ontario. McCombie and Fry (1960) used data on this population collected between 1953 and August 1958 during which period varying fractions of the catches in different nets were sampled. From August 1958 to 1963 total catches were sampled and this greatly simplifies subsequent calculations. We restrict consideration here to this second series of data. Except with respect to size of sample, sampling methods remained as described by McCombie and Fry.

Altogether 6951 whitefish were sampled. Numbers of fish of different lengths taken by different gears are shown in Appendix I. Only 50 yards of net were used for mesh sizes under 2 inches, while 150 yards were used for all meshes 2 inches and larger. Numbers caught in the smaller meshes were tripled to make the data comparable and it is the corrected data that are entered in Appendix I.

I. Direct Method

Cucin and Regier (1966) described and used this method with a whitefish population in southern Georgian Bay; a summary follows. In a single short fishing season 1188 whitefish were caught in pound nets, tagged, and released. The fish ranged from 12 to 23 inches long. Gill nets within 10 miles of the pound nets recaptured 101 of these fish within 3 months. All gillnets were 4½-inch mesh. The tags used likely did not increase vulnerability appreciably. Data on lengths at recapture were not available but growth data indicated that increase in length averaged about 0.25 inch during the period of freedom and rarely exceeded 0.5 inch for individual fish.

Length–frequency distributions of the released and recaptured fish were stratified by 0.5-inch intervals and the selectivity of gill nets estimated by comparing these frequencies (Fig. 2).

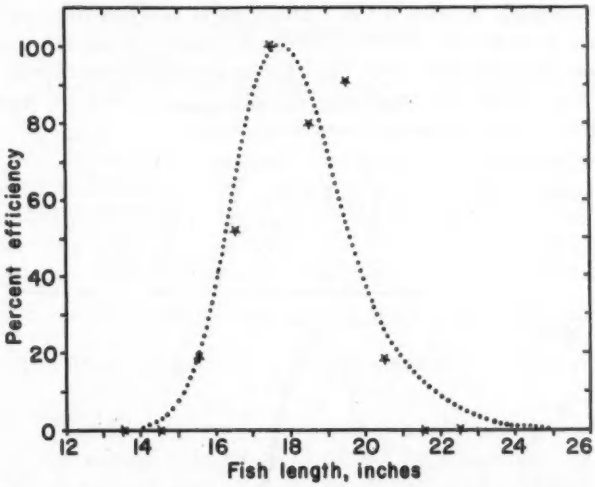

FIG. 2. Stars indicate data obtained for estimating selectivity of 4.5-inch mesh by the direct method, data from southern Georgian Bay; dashed curve is our "standard," that estimated by the computational method using a skew-normal model.

II. Indirect Methods

A. Type A curves

1. *Normal model.* Results obtained by McCombie and Fry (1960) using a graphical method (see below) showed that neither of the normal models described above were suitable for Type A curves. This was corroborated by results from other methods given below. Nevertheless, we did estimate selectivity of the 4.5-inch mesh by comparing catches of 4.5- and 4.0-inch meshes and also

4.5- and 3.5-inch meshes, under the assumption that the variance of the selection curves of all three were constant. Results are shown in Fig. 3.

2. *Olsen exponential model.* As indicated earlier, the right descending arm of this model never reaches zero though it may approach it closely before again ascending to infinity. We used the whitefish data in Appendix I to estimate the selectivity curve for 4.5-inch mesh by comparing the catches of the 4.0- and 4.5-inch mesh. The data were stratified by 0.5-inch intervals of fork length to reduce variability in the ratios $R_{i+1,i,j}$. Figure 4 shows the estimated selectivity. It is clear that this model is unsuitable for these combinations of l_j and m_i. We did not search for transformations that might have led to data with which the model would be acceptable.

3. *Gamma model.* We had the analysis using this method programmed for the computer using data in Appendix I. Where necessary, we pooled data from adjacent strata, j, so that $n_{ij'} + n_{i+1,j'} \geq 50$ in all strata used for computing. (Here j' indexes the new strata.) This greatly reduced the incidence of zero numerators or denominators, both disallowed in the analysis, as well as increased the precision of the ratios $R_{i+1,i,j}$. Unequal sample size was taken into account in computing the regression of $lnR_{i+1,i,j'}$ on $lnl_{j'}$ by weighting each by the inverse of its approximate variance, where

$$\sigma^2 (R_{i+1,i,j'}) = \text{var}\left[ln\left(\frac{n_{i+1,j'}}{n_{ij'}}\right)\right] = \frac{n_{i+1,j'} + n_{ij'}}{(n_{i+1,j'})\ (n_{ij'})}.$$

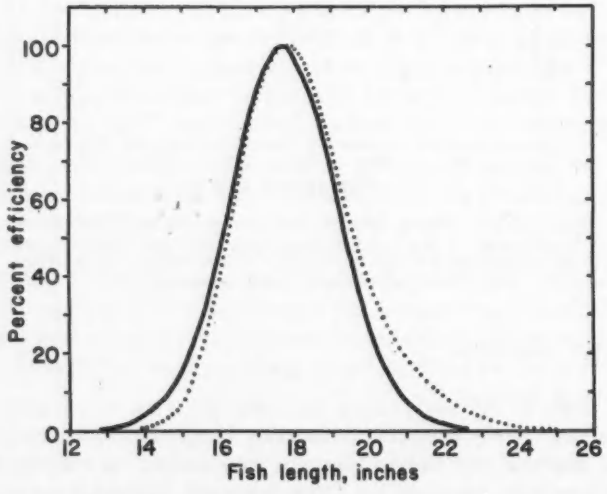

FIG. 3. Continuous curve for 4.5-inch mesh estimated by Holt (1963) method with normal model using data from 4.5- and 4.0-inch mesh, dashed curve is our standard.

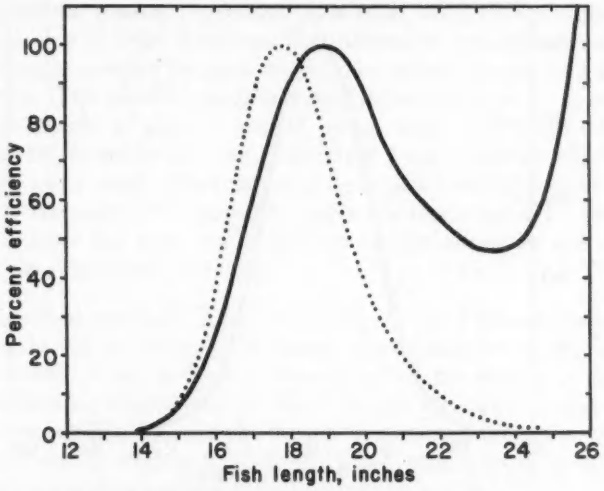

FIG. 4. Continuous curve for 4.5-inch mesh estimated using the Olsen exponential model with data from 4.5- and 4.0-inch mesh, dashed curve is our standard.

In spite of these attempts to increase the precision of the estimates, this approach yielded no unique estimate of selectivity. In fact in some cases the computer program resulted in negative estimates of α and β. Thus these data obviously deviated from the gamma model. However, if a particular $k_{i+1,i}$ is assumed we may at least estimate the selectivity under this additional assumption. Using data from 4.5- and 5.0-inch meshes, and assuming $k_{i+1,i} = \frac{\bar{l}_i}{m_i} = \frac{17.7}{4.5} = 1.97$, then Fig. 5 depicts the resulting estimate using the gamma model.

TYPE B CURVES

1. *Graphical method of McCombie and Fry.* Rather than use this method with the 1959–63 data we shall compare McCombie and Fry's result from the 1954–58 data with our result using the computational method and skew-normal model. Figure 6 shows those estimates for 4.5-inch mesh. Observed differences were due to at least two causes. McCombie and Fry's estimate for this mesh size was largely an extrapolation from Type B curves of length strata from 10 to 16 inches. The addition of 5-inch mesh in 1958 permitted this range to be extended to about 18 inches for our estimates. Analysis of the moments of the Type B curves with the more recent data showed that McCombie and Fry's basic model was violated, at least as m_i and l_j became large. Specifically, mean and variance were found to be curvilinearly related to l_j, not linearly as is implicit in their approach. Secondly, these authors used 0.5-inch strata of fork length while our estimate was based on 0.1-inch strata. The broader strata resulted in a somewhat flatter curve, as is apparent in the comparison.

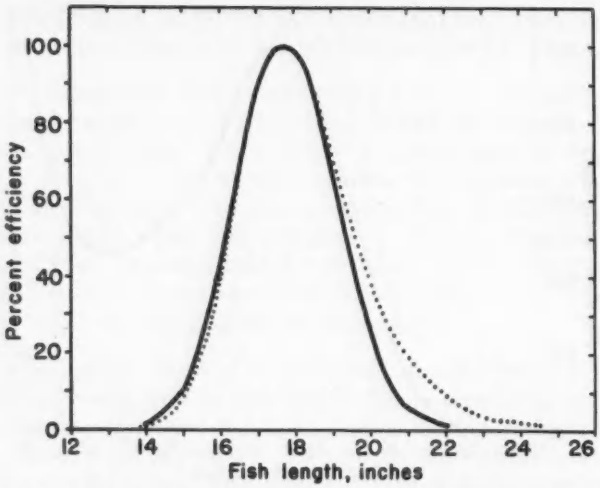

FIG. 5. Continuous curve for 4.5-inch mesh estimated using the gamma model with data from 4.5- and 5.0-inch mesh assuming k = 1.97, dashed curve is our standard.

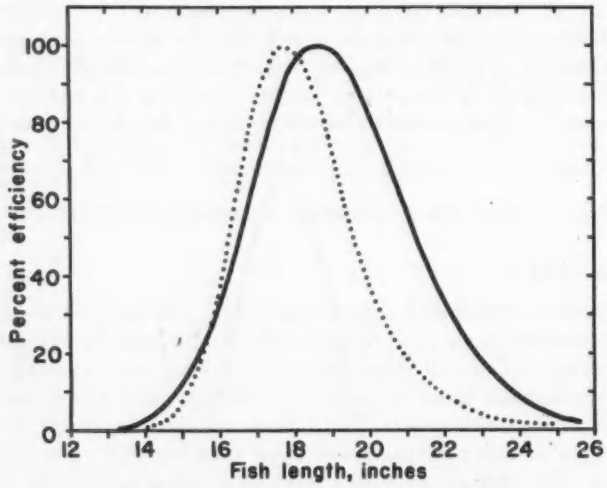

FIG. 6. Continuous curve for 4.5-inch mesh estimated by McCombie and Fry (1960) using 1954–58 data, dashed curve is our standard based on 1959–63 data.

The agreement between McCombie and Fry's results and ours was much better for 2–3.5 mesh than for 4.5 mesh. But here too the former were appreciably flatter.

2. *Graphical method, "variance" constant.* We stated earlier (in the general discussion of Type B curves) that unless the various mesh sizes form a regular series the analysis becomes messy. The data in Appendix I are not in a regular series. The present method could estimate Type B curves for fish between the lengths of about 7 and 11 inches using mesh sizes increasing by ¼-inch intervals. In addition it could estimate Type B curves with fish from 7 to 17 inches using mesh sizes increasing by ½-inch intervals, i.e. 1.5, 2.0, 2.5, 3.0, 3.5, 4.0. We used both approaches since the former gave far more reliable results for shorter fish than the latter, but restrict ourselves here only to the analysis of data by ½-inch intervals.

We require an estimate of $f(l_j)$ where $\bar{m}_j = f(l_j)$. Preliminary analysis had shown that the Type B selectivity curves were approximately symmetric and thus $\bar{m}_j$ = mean of m_i for fixed j = mode of m_i for fixed j = μ_j. We drew histograms showing the number of fish of length l_j caught in each mesh size, m_i, and by inspection located the length corresponding to the approximate mode, $\bar{\mu}_i$. We set $\hat{\bar{m}}_j = \hat{\mu}_j = a + bl_j + cl_j^2$ and estimated a, b, and c by the least squares regression method and obtained the values

$$\hat{\bar{m}}_j = 0.649 + 0.08485l_j + 0.007551l_j^2.$$

Solution of this equation then yielded an estimate of the mean at each l_j.

If, as we assume, the "variance" of Type B curves does not change rapidly with l_j and thus is approximately constant for short ranges of l_j, then we may plot the frequency distributions of n_{ij} vs. m_i for a series of l_j and superimpose them by correcting the m_i according to the relationship estimated for $\hat{\bar{m}}_j$. For example, suppose we decide to estimate a Type B curve at 11.5 inches using fish of length 11.0–12.0 inches. Table I shows how adjustments, $\hat{\bar{\mu}} - \hat{\mu}_j$, were estimated for the m_i for each l_j in this stratum. A plot of n_{ij} vs. corresponding $m_i + \hat{\bar{\mu}} - \hat{\mu}_j$ then yields a scatter of points to which a Type B curve may be fitted.

(If the square root of the "variance" does in fact increase approximately linearly with l_j, then the curve estimated above is still relatively unbiased at the mid point of the range since underestimates at the shorter lengths are approximately balanced by overestimates at the longer lengths.)

The next decision to be made is the number of l_j to include in a particular stratum and the lengths at which to center the strata. It will make the task of deriving Type A curves from Type B curves simpler if we choose to center the strata at lengths near the mode of the Type A curves. We may obtain estimates of these modes by solving the relationship $\hat{\mu}_i = f(l_j)$ estimated earlier for l_j at the specified μ_i. Denote the strata mid points as $\hat{l}_i$ and divide the array of l_j's to assign about equal numbers of adjacent l_j's to each $\hat{l}_i$. Calculate adjustments for m_i as in Table I and plot Type B curves.

TABLE I. Method of calculating adjustments for m_i for short ranges of l_j.

l_j	$\hat{\mu}_j$	$\hat{\bar{\mu}} - \hat{\mu}_j$
11.0	1.847	0.127
11.1	1.872	0.102
11.2	1.898	0.076
11.3	1.923	0.051
11.4	1.948	0.026
11.5	1.974	0
11.6	2.000	−0.026
11.7	2.026	−0.052
11.8	2.052	−0.078
11.9	2.079	−0.105
12.0	2.106	−0.131

The most critical part of estimating Type B curves is the problem of locating the maximum points, since all Type B curves will later be standardized (according to an assumption stated earlier) to have ordinates of the maximum points, r_i, equal. We estimated r_i of all Type B curves iteratively. From the plots of n_{ij} vs. adjusted m_i we determined $\tilde{r}_i$, then plotted $\tilde{r}_i$ vs. m_i, drew a smooth curve and estimated $\hat{r}_i$ from it. Taking into account the $\hat{r}_i$, we modified the Type B curves, replotted $\hat{r}_i$ vs. m_i, etc. until we obtained a satisfactory fit.

Type B curves were then standardized by dividing all ordinates by corresponding $\hat{r}_i$. Points on the Type A curves were estimated as follows. Designate $m(a, \hat{\mu}_i; x)$ as the mesh size, in the ascending arm of the Type B curve with mode at $\hat{\mu}_i$, at which x is the relative efficiency of capture. Similarly

TABLE II. Strata mid points and limits chosen for the whitefish data.

m_i	l_i	Strata limits
1.75	7.70	7.0– 8.2
2.00	8.89	8.3– 9.4
2.25	9.99	9.5–10.5
2.50	11.02	10.6–11.4
2.75	11.98	11.5–12.4
3.00	12.90	12.5–13.4
3.50	14.61	13.8–15.3
4.00	16.18	15.4–16.9

$m(d, \hat{\mu}_i; x)$ relates to the descending arm. For a and a particular value of x, plot $m(a, \hat{\mu}_i; x)$ vs. $\hat{\mu}_i$ and fit a curve or straight line to the points. We drew separate curves for $x = 0.1, 0.3, 0.6, 0.9$, and 1.0 corresponding to first a and then d. Figure 7 shows the result. We found that the nine different series of points could be fitted reasonably well by a family of lines radiating out from the origin.

We may use the estimated relationship between $\hat{\mu}_i$ and l_j to locate a scale of length of fish on the abscissa. Then picking a particular value on the ordinate, e.g. Y = 2.5, we may read off the fish lengths at which this mesh size has a relative efficiency of 0.1, 0.3, 0.6, 0.9, 1.0, 0.9, 0.6, 0.3, and 0.1. A plot of these data vs. fish lengths is the final estimate of the Type A curve.

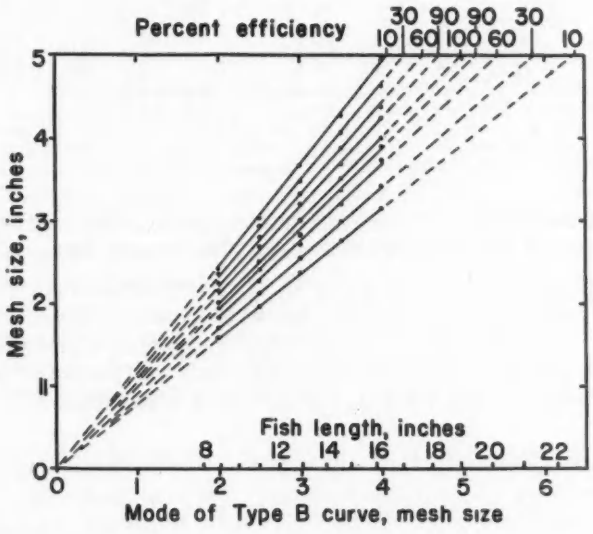

FIG. 7. Curves for deriving Type A curves from Type B curves estimated by the graphical method with "variance" constant within short size ranges.

It is clear from Fig. 7 that we can obtain an estimate of the Type A curve for 4.5-inch mesh only if we extrapolate seven of the nine lines drawn there. Figure 8 shows that estimate. The agreement with our standard of comparison is very close in the ascending arm but the relative discrepancy increases towards the tails of the descending arm. The discrepancy is thus in the region where both curves are based on extrapolations and where the extrapolations were made in a different manner. In the region of interpolation, e.g. mesh sizes of 2.5–3.5 inches, the agreement by these two methods was very close indeed, with a maximum relative discrepancy of only 10% in the 3.0-inch mesh.

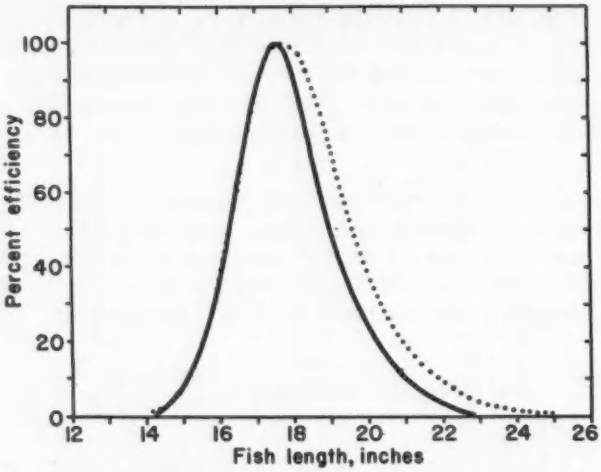

FIG. 8. Continuous curve for 4.5-inch mesh estimated by our graphical method with "variance" constant within short size ranges, dashed curve is our standard curve.

3. *Computational method, skew-normal model.* The comments in the first paragraph of the preceding section are also relevant here.

To estimate the relationships of $\hat{\bar{m}}_j$, $\hat{\sigma}_j^2$, and $\hat{q}_j$ in the Type B curves to l_j we used step-wise multiple regression methods arbitrarily limiting the polynomial to a power of four and using an F corresponding to a probability level of 0.95. Searle and Primer (1964) have described the computer program for step-wise regression. Following are the estimated relationships:

$$\hat{\bar{m}}_j = 1.99427 + 0.0266212l_j^2 - 0.0000138331l_j^4$$

$$\hat{\sigma}_j^2 = -0.07133 + 0.00283425l_j^2$$

$$\hat{q}_j = 0.00573982.$$

Three points are of interest here. First $\hat{\bar{m}}_j$ is not a linear function of l_j, $\hat{\sigma}_j$ is almost in direct proportion to l_j, and $\hat{q}_j$ is not related to l_j. It is the first of these three that deviates from the assumption in the McCombie-Fry approach and this is a probable reason for the discrepancy between their results (Fig. 6) and ours.

The computer output is shown in Appendix II, and the results are shown in Fig. 9.

DISCUSSION

We believe the results from the computational method using the skew-normal model for Type B curves to be our most reliable estimates. Discrepancies

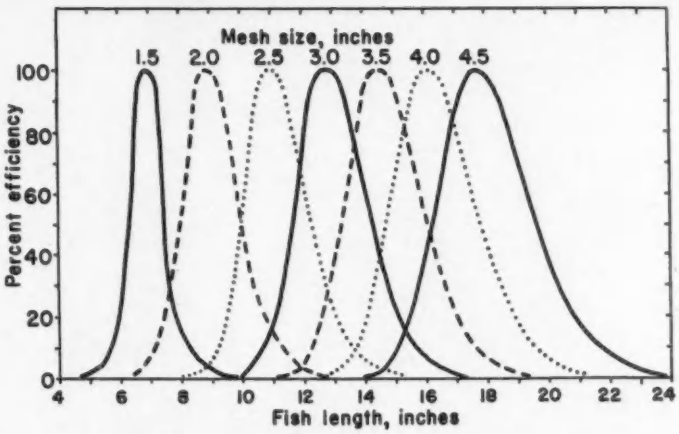

FIG. 9. Selectivity curves for various mesh sizes estimated by our computational method with skew-normal model, i.e. our "standard" curves.

between these estimates and those of other methods were traced either to assumptions in other methods that were violated by our data (normal, Olsen, gamma, McCombie-Fry, graphical method with "variance" constant) or to insufficient data (direct method). Two other methods (Ishida, Gulland-Harding) did not yield unique estimates. We continue to have reservations about our "most reliable estimates," especially in respect to the assumption that at peak efficiency all mesh sizes are equally efficient. This assumption is common to all the methods other than a direct method using more than one mesh at the same time. Experiments with the latter method should be done to resolve this problem.

"Standard gangs" of gill nets are often used for survey purposes. Mesh sizes are usually chosen to be in arithmetic series, 1, 1¼, 1½, etc. If equal lengths of each mesh size are taken, then Fig. 9 shows that total efficiency of such a gang increases with length of fish, and thus may well be an inefficient design. Using data in Fig. 9 it is possible to derive a series of mesh sizes such that the total efficiency is roughly equal over all lengths of interest. For example, we may choose adjacent mesh sizes so that the larger length at which the smaller mesh has a relative efficiency of 50% coincides with the smaller length at which the larger mesh has the same relative efficiency. Figure 10 shows plots of mesh size at which 50% of fish are retained (relatively) vs. fish length, for both ascending and descending arms of the selectivity curves. To obtain a series of mesh sizes of approximately equal efficiency towards whitefish from 7 to 18 inches we start with a mesh size of 1.5 inches and follow the steps (Fig. 10) and derive the series 1.5, 1.8, 2.3, 2.9, 3.7, 4.7. We estimated the relative efficiency of such a series towards whitefish by completing Fig. 10 for other levels of efficiency (5, 10, 20, 40, 60, 80, 90) and summing the efficiencies

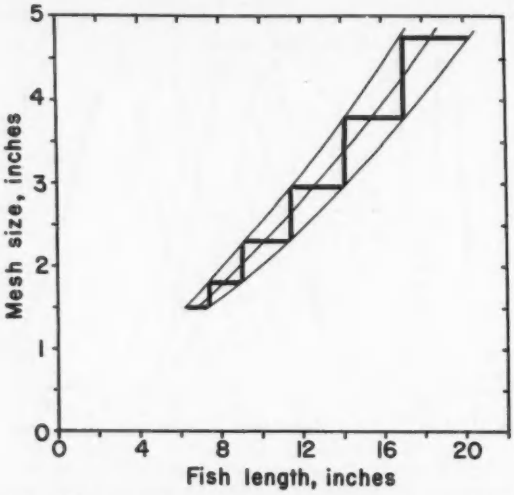

FIG. 10. Method of deriving mesh sizes of a standard gang of nets to yield approximately equal efficiency toward whitefish of length 7–18 inches. Top curve represents relative efficiency of 50% in left arm of selectivity curve, middle curve represents 100%, and bottom curve 50% in right arm.

of the various nets to fish of each length stratum. With mean efficiency over this length range taken at 100, maximum deviations were found to be 88 and 108. By comparison the standard gang described by McCombie and Fry (1960), i.e. 1.5, 1.75, 2.0, 2.25, 2.5, 2.75, 3.0, 3.5, 4.0, 4.5 has deviations from a mean of 100 of 78 and 121. The latter series, really two arithmetic series, uses 10 nets as compared to six in the series we suggest.

It should be pointed out that the series we suggest is tailored to our estimates for lake whitefish. We do not recommend its adoption for general surveys because the choice of an efficient series should take into account selectivities towards other species of fish which the nets are also intended to sample. Judging from results of McCombie and Fry (1960), Berst (1961), Ishida (1962, 1964), and others, and considering that the implicit assumptions in their methods are approximately correct as verified by those of our methods which were not based on these assumptions, we conclude that in general an arithmetic series or group of such series will not be as efficient as a series of the sort we have derived.

The series we used, 1.5, 1.8, 2.3, 2.9, 3.7, 4.7, closely resembles the geometric series 1.4, 1.8, 2.3, 2.9, 3.7, 4.7, obtained by expanding $1.40(1.1275)^x$ with $x = 0, 1, 2, 3, 4, 5$. Larger and smaller values of the latter series are: 0.4, 0.5, 0.7, 0.9, 1.1 and 6.0, 7.7, 9.8.

Let us define a net's "total efficiency" with respect to numbers of fish as $L_i = \sum_j S_{ij}$ and with respect to weight as $W_i = \sum_j S_{ij} w_j$. Total efficiencies of

different nets would be in direct proportion to the expected number of fish or weight of fish caught in different meshes if there were equal numbers of fish in each length stratum (also assuming our selectivity estimates are accurate). We found that $L_i = 12 + 5.5m_i$ for $2 \leq m_i \leq 4.5$ and probably sigmoid to the origin for $m_i < 2$. Similarly $W_i = 0.80m_i^{3.2}$ for $2 \leq m_i \leq 4.5$ if $w_j = 0.0002401l_j^{3.2093}$ as found by Cucin and Regier (1966). These relationships show that total efficiency increases with mesh size, e.g. W increases from about 7.5 for 2-inch mesh to 100 for 4.5-inch mesh and about 200 for 5.5-inch mesh.

Cucin and Regier (1966) have used the estimates of selectivity derived here to correct estimates of mean length of year-classes at various ages for sampling bias. They have shown that the nature of the selectivity curve strongly influences the catch curve and consequently introduces errors into estimates of mortality based on catch curves. They also drew attention to the fact that the usual analyses of catch-effort statistics do not take into account the relationship of total efficiency to mesh size.

ACKNOWLEDGMENTS

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Mrs N. Earle and E. C. Townsend of the Cornell Computing Center wrote our computer programs; S. R. Searle advised on programming difficulties.

G. S. Overton of Emory University advised on estimation methods.

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APPENDIX I. Numbers of fish of various lengths taken by gill nets of various mesh sizes in experimental sets in South Bay, Manitoulin Island, during the late summers and autumns of 1959–63. (Data courtesy of Research Branch, Ontario Department of Lands and Forests.)

Fork length (*inches*)	Mesh size (*inches*)											
	1	1½	1¾	2	2¼	2½	2¾	3	3½	4	4½	5
4.3	3											
4.4	6											
4.5	6											
4.6	6											
4.7	3											
4.8	6											
4.9	3											
5.0	9											
5.1	3											
5.3	3											
5.4		3										
5.5		3										
6.3		6										
6.5		6	3									
6.6		3										
6.7		6		1								
6.8	3	9	3									
6.9		9										
7.0		9	3		1	1						
7.1		6	9									
7.2		21	27									
7.3		21	24	1								
7.4		3	30									
7.5		9	36	1		1						
7.6		12	48	1								
7.7		6	36	8								
7.8		6	69	6								
7.9		6	45	10								
8.0		12	54	18								
8.1			48	14								
8.2		3	42	22	1							
8.3		21	33	1								
8.4		15	22									
8.5		6	18	32	5							
8.6			9	35	2	1						
8.7		3	3	23	2							
8.8			15	23	5							
8.9			6	7	6							
9.0		3	15	43	21	1		1				
9.1			9	33	17	1						
9.2			12	39	29	3						
9.3			3	37	42	6						
9.4			6	27	46	12	2					
9.5			15	49	43	22	2	1				
9.6			6	36	59	16	1					
9.7			3	26	66	19	8					
9.8			6	21	54	27						
9.9			3	32	48	25	1					
10.0				21	62	41	5					
10.1			6	22	38	42	1					
10.2			6	27	49	44	9					
10.3		3		19	41	43	8	2				
10.4				14	23	39	8					
10.5			3	16	37	36	13	2				
10.6			6	5	15	31	15	1				
10.7		3		11	24	23	13	1				
10.8			3	13	21	30	13	4				
10.9				7	17	20	9	4				
11.0				7	22	42	25	6				
11.1				4	20	30	17	7	1			
11.2				6	16	40	38	8	1			
11.3			3	3	21	38	24	16				
11.4			2	2	12	38	24	16				
11.5					11	34	38	29				
11.6				2	11	29	24	16				
11.7				3	9	41	31	24				
11.8				3	7	37	38	25				
11.9					6	22	27	24	1			
12.0				3	10	36	30	27				
12.1					4	23	29	27	6			

12.2	1	3	25	26	28	2			
12.3	1	5	13	25	37	4			
12.4		4	14	12	22	1			
12.5		7	13	25	32	3			
12.6		1	5	8	24				
12.7		1	8	24	26	3			
12.8		1	11	21	25	9			
12.9		1	6	7	20	4	1		
13.0	1	5	17	29	53	7			
13.1		1	2	9	21	2			
13.2	1	1	2	6	16	10			
13.3			3	10	11	8	1		
13.4		1	3	9	15	8			
13.5		2	1	14	21	14			
13.6			1	6	11	11		1	
13.7			1	8	13	12			
13.8				6	9	21	4		
13.9			1	4	2	6	4		
14.0			1	2	12	24	3		
14.1		1	2	5	8	13	2	1	
14.2				7	11	16	4		
14.3			1	4	6	15	6		
14.4		2		3	7	11	2		
14.5				5	6	18	7		
14.6			2	1	4	24	3		1
14.7			2		8	21	14	2	
14.8		1		1	1	28	8	1	
14.9				3	3	14	10	1	
15.0				3	7	16	12	1	1
15.1				2	5	20	13	2	
15.2		1	1	1	1	30	9	1	
15.3					3	13	16	5	
15.4					1	8	17	2	
15.5			1		2	9	13	8	
15.6					1	8	20	3	
15.7				2	2	9	16	3	1
15.8				1	1	10	15	6	2
15.9				1	1	5	17	5	1
16.0		1				10	18	5	
16.1						2	13	5	1
16.2					1	9	13	9	
16.3						5	19	5	
16.4					1	4	8	7	
16.5						8	14	8	3
16.6				2	1	5	8	4	2
16.7						5	8	11	
16.8					1	5	16	7	4
16.9						2	8	9	
17.0				1		4	8	10	
17.1						5	4	8	
17.2						3	9	9	3
17.3	1					2	9	12	2
17.4							3	12	1
17.5							8	10	6
17.6						1	3	4	3
17.7						1	4	4	1
17.8					1	1	9	10	3
17.9							4	4	3
18.0						1	3	8	2
18.1						1	7	6	3
18.2						1	4	6	4
18.3					1	1		6	7
18.4			1				4	5	5
18.5							4	4	5
18.6							3	7	5
18.7							2	4	3
18.8						1	1	3	1
18.9							1	5	4
19.0							7	2	5
19.1				1		1	4	3	2
19.2				1		1	1	4	4
19.3							1	7	5
19.4							1	1	4
19.5								3	2
19.6							2	4	4
19.8							1	1	
19.9								4	
20.0									1
20.1							2	1	2
20.2									1
20.3								1	
20.4							1		
20.5									1
20.6	1								
23.0									1
24.1								1	

APPENDIX II. Gillnet selectivity toward lake whitefish estimated by the computational method with the skew-normal model. Data below dashed line are based on extrapolation. Multiply all data by 10^{-3}.

Fork length	Mesh size (*inches*)																
(*inches*)	1	1¼	1½	1¾	2	2¼	2½	2¾	3	3¼	3½	3¾	4	4¼	4½	4¾	5
4.09	779	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5.35	0	047	039	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6.57	0	024	871	241	001	0	0	0	0	0	0	0	0	0	0	0	0
7.74	0	004	227	992	344	009	0	0	0	0	0	0	0	0	0	0	0
8.87	0	001	036	436	1000	440	037	001	0	0	0	0	0	0	0	0	0
9.94	0	0	005	096	565	1000	534	086	004	0	0	0	0	0	0	0	0
10.96	0	0	001	016	160	637	1000	621	153	015	001	0	0	0	0	0	0
11.94	0	0	0	002	033	218	680	1000	693	227	035	003	0	0	0	0	0
12.86	0	0	0	0	006	054	270	712	1000	748	299	064	007	0	0	0	0
13.74	0	0	0	0	001	012	081	321	742	999	785	360	097	015	001	0	0
14.57	0	0	0	0	0	002	021	113	374	775	1000	805	405	127	025	003	0
15.35	0	0	0	0	0	001	005	035	152	435	813	1000	808	430	151	035	005
16.08	0	0	0	0	0	0	001	010	056	203	505	858	998	796	435	163	042
16.76	0	0	0	0	0	0	0	003	020	087	269	587	906	990	766	421	164
17.39	0	0	0	0	0	0	0	001	007	036	133	352	679	952	969	719	388
17.98	0	0	0	0	0	0	0	0	003	015	064	199	456	779	987	930	652
18.51	0	0	0	0	0	0	0	0	001	007	031	110	291	580	875	1000	865
19.00	0	0	0	0	0	0	0	0	0	004	016	062	182	412	716	955	979
19.43	0	0	0	0	0	0	0	0	0	002	009	036	116	289	562	849	997
20.16	0	0	0	0	0	0	0	0	0	0	003	014	051	148	339	614	880
20.69	0	0	0	0	0	0	0	0	0	0	001	007	028	088	221	448	727
21.12	0	0	0	0	0	0	0	0	0	0	001	004	017	056	152	334	593

NOTES

Relationship Between Size and Maturity in the Spottail Shiner, *Notropis hudsonius*[1]

The spottail shiner, *Notropis hudsonius* Clinton, is a small cyprinid common in lakes and rivers throughout most of North America ranging from Kansas, Iowa, and Illinois (Hubbs and Lagler, 1949) northward to the MacKenzie River (Wynne-Edwards, 1952), and in the east from Virginia to the Hudson River (Eddy, 1957).

Life history studies on populations in Clear Lake, Iowa, by McCann (1959) found a daily summer growth increment of 0.6–0.18 mm/day for age groups I and II, respectively. Maturity was attained after 1 year when the average total length was 77 mm. The life span was 4 years. In Red Lake, Minnesota (Smith and Kramer, 1964), maturity was attained after 2 years when the average total length was 85 mm. Here the fish lived for 5 years. The results of these studies and the present one indicate a relationship between size and maturity.

The original data for this report were obtained as part of a life history study for this species in Nemeiben Lake, Saskatchewan. This lake, considered oligotrophic by Koshinsky (MS, 1964), is located on and receives its runoff from the southern part of the Precambrian Shield.

Summer growth rate of small shiners was estimated from shifts in the average lengths of year-classes throughout the summer. Lengths were obtained from the modes which could be clearly seen on length frequency histograms prepared from measurements of 1300 fish taken in seine hauls at intervals throughout the summer of 1960. The validity of the year-class modes was checked by scale annulus counts of subsamples of fish. All specimens were examined to determine the state of maturity. Similar observations on growth were made on spottail shiner populations from Crooked Lake located in southern Saskatchewan.

All of the mature spottail shiners seined before July 10 were found to be in spawning condition and all those seined after July 11 were spent, suggesting that spawning took place July 10–11. The mature fish left the sandy shoals immediately after spawning. The age group II shiners left about July 17 and the age group I fish left about July 26. The age group 0 were first seen on August 2 at which time they had a modal length of about 22 mm.

Fish from the more northern lakes in Saskatchewan were smaller than those of similar ages in the more southern lakes of Iowa and Minnesota, and the average annual growth increment of the prespawning fish is less (Table I).

[1]Based on a thesis submitted in partial fulfilment of the requirements for the degree of Master of Science at the University of Saskatchewan.

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TABLE I. Comparative growth rate of spottail shiners from different areas (numerals in bold type indicate maturity).

Lake	Location	Modal total length in spring				Average growth increments assuming 4 mm on hatching		
		I	II	III	IV	I	II	III
Nemeiben Lake, Sask.	55°20′N lat, 105°30′W long	38.9	62.2	**83.1**		34.9	23.3	20.9
Crooked Lake, Sask.	50°30′N lat, 102°30′W long	47.0	**68.5**	**90.4**		43.0	21.5	21.9
Red Lake, Minn.	48°00′N lat, 95°00′W long	56.4	**85.4**	**100.0**	**105.0**	52.4	29.0	15.0
Clear Lake, Iowa	43°00′N lat, 93°30′W long	**76.7**	**98.2**	**107.9**		72.7	21.5	08.0

A north–south difference in the pattern of growth occurred as well. In the Nemeiben Lake population about 43% of the final length (age IV) is reached by the age I shiners whereas in the Clear Lake population about 70% of the average age IV size is reached by the age I fish. The same proportion is about 50% for Crooked Lake and Red Lake. Evidence of this difference was also seen by the daily summer growth increments which, for the Nemeiben Lake population, was 0.3 mm/day for ages I and II and was given by McCann (1959) as 0.6 and 0.18 mm/day for ages I and II, respectively.

Spawning date was also affected by latitude. In Nemeiben Lake spawning took place on July 10–11 in 1960; in Red Lake, the date of spawning of *N. hudsonius* was June 15 (Smith and Kramer, 1964); and in Clear Lake, it was May (McCann, 1959).

Gonads of all shiners taken from Nemeiben Lake during the summer of 1960 showed that no fish smaller than 67 mm in total length was mature, indicating that spawning fish were age III or older.

A small sample (225) of *N. hudsonius* taken from Crooked Lake in June showed that all individuals over 67 mm were in spawning condition, while those 64 mm or less were immature. Year-class lengths determined from length frequency histograms indicate that the spawning fish were age II or older. In Red Lake population (Smith and Kramer, 1964) age I had a mean total length of 56.4 mm while age II fish had a mean length of 85.4 at annulus formation. Spawning first took place at age II. In Clear Lake, shiners after 1 year of life had a mean total length of 72 mm or over. Spawning first took place at age I (McCann, 1959).

Sexual maturity, therefore, seems to occur only after a total length of approximately 68 mm is reached. The annual growth increments of prespawning fish are less in the more northern lakes; and the age when spawning first

occurs varies from the second summer (Clear Lake) to the fourth summer (Nemeiben Lake).

The phenomenon of the timing of an event in the life history of an animal being a function of growth rate is known to occur in the Atlantic salmon, *Salmo salar*. In this case it is smoltification (Jones, 1959). In the spottail shiner maturity may be a function of both growth rate and size, or some factor common to them both.

There is no evidence of increased life span for the northern populations as the oldest specimens found from Nemeiben Lake had four annuli (age IV) as did the Clear Lake population. However, few large fish were collected. Mature shiners left the sandy shoals immediately after spawning and, during the remainder of the summer, could only be taken by a gill net set in 4–7 m of water. If the maximum age does in fact remain the same regardless of latitude the reproductive potential of the northern fishes would be considerably reduced.

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Some Scale Characters of the Ozernaya Sockeye Salmon[1]

A collection of 720 readable sockeye scales from the domestic fishery at the Ozernaya River mouth over a period of 10 years (1951–60) was made available to the writer by Professor P. A. Moiseev, Vice-Director of the All-Union Research Institute of Marine Fisheries and Oceanography (VNIRO).

The scales had been taken between the dorsal fin and the lateral line. In North American salmon research, the region midway between the dorsal and adipose fins is preferred, the scales being selected from the first or second row above the lateral line.

The length of stay and growth of the fish in fresh water were determined from the lacustrine portion of the scales.

Lacustrine age. Among the 720 scales in the collection, none was found with only one freshwater annulus. The proportion of *2.* salmon varied from 70.2 to 97.1% over the entire period and averaged 82.2%, the remainder consisting of *3.* fish.[2] Egorova et al. (1962) indicate a similar age composition for sockeye from Lake Kuril (Ozernaya River) during 1940–59 in annual runs ranging from 3 to 9 million fish.

In areas with mixing of Asian and North American salmon no fish of the important *1.* group can be assigned to the Ozernaya system.

In more restricted mixing areas, where only Asian and Bristol Bay sockeye salmon intermingle, the *3.* fish can be considered of Asian origin and primarily from the Ozernaya system. During the years 1951–59, less than 1% of *3.* sockeye salmon returned to Bristol Bay (Table I).

TABLE I. Occurrence of *3.* sockeye salmon in Bristol Bay catches.[a]

District	Total catch, 1951–59 (1000s)	Number of *3.* fish in catch (1000s)	Per cent of *3.* fish in total run
Nushagak	7,521	0.75	0.01 (1946–59)
Naknek–Kvichak	33,629	60.53	0.18 (1957–63)
Egegik	7,991	278.88	3.49 (1957–62)
Ugashik	4,145	38.97	0.94 (1948–57)
Total:	53,286	379.13	0.71 (weighted)

[a]Source: Nushagak from Mathisen et al. (1963); Naknek, Kvichak, and Egegik from personal communication with Dr C. DiCostanzo, Bureau of Commercial Fisheries, Auke Bay, Alaska; Ugashik from Kerns (1963).

[1]Contribution No. 209, College of Fisheries, University of Washington.

[2]Age notation is according to Koo (1962a), where *1.* denotes a fish which has spent one winter in fresh water, etc.

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As for sockeye salmon with two complete lacustrine annuli, all known stocks of sockeye salmon may contribute to the high seas catches.

Lacustrine growth pattern. The average number of circuli formed in the first year for *2.* fish is 1.19 circuli greater than for *3.* fish, and in the second year for *2.* fish is 1.69 circuli greater than for *3.* fish (Table II and Fig. 1). Spring growth before seaward migration in *2.* fish is, on the average, better than in *3.* fish, 1.67 and 1.23 circuli, respectively. Thus, the *3.* salmon lag behind the *2.* salmon during the first and second years of life, but the differences are so small that the average total number of circuli in *3.* fish at the time of migration is consistently greater than in *2.* fish.

In the second year of life, the average distance between circuli on the enlarged scale image was nearly the same in both age groups of young salmon (Fig. 2). Even in the third year of life of *3.* fish, the value of this parameter remained unchanged, and in all cases was only about 64% of the average value for the first year of life. After the first year, the distance between circuli decreased and remained constant, regardless of whether the salmon spent only one or two additional years in fresh water.

The circulus count and general appearance of the freshwater portion of Ozernaya sockeye scales differ from that commonly found in Bristol Bay sockeye (Fig. 3). Burgner (unpublished data) examined scales taken in the Nushagak fishery in 1957 and found an average formation of 15.27 circuli during the first year in fresh water. This figure is not directly comparable with those in Table II because the methods used in taking scales differ. But as Koo (1962b) has demonstrated, scales taken under the dorsal fin may

TABLE II. Circulus counts of Ozernaya sockeye salmon.

	2. fish				*3.* fish				
		Average no. circuli formed				Average no. circuli formed			
Year of return	Sample size	1st year	2nd year	In year of smolt migration	Sample size	1st year	2nd year	3rd year	In year of smolt migration
1951	60	6.10	8.03	1.72	2	4.00	5.50	5.50	1.50
1952	67	5.81	8.88	1.69	2	3.50	6.50	8.50	0.50
1953	66	6.64	8.68	1.82	9	5.78	7.56	6.44	1.11
1954	45	5.82	9.42	1.09	19	5.89	7.00	8.11	0.89
1955	67	5.16	9.12	1.12	14	4.36	7.14	6.93	1.00
1956	56	5.80	8.54	0.98	17	4.24	7.12	7.35	0.88
1957	52	5.62	7.60	0.90	27	4.22	6.89	7.00	0.93
1958	49	6.00	8.63	1.57	10	4.50	6.30	7.90	1.40
1959	55	7.13	9.09	2.78	22	5.18	7.68	7.82	2.18
1960	75	5.95	8.84	1.80	6	5.17	7.50	6.67	1.83
All years combined	592	6.00	8.69	1.57	128	4.81	7.10	7.36	1.23
Variance		3.46	3.23	1.49		2.17	1.87	2.25	1.06

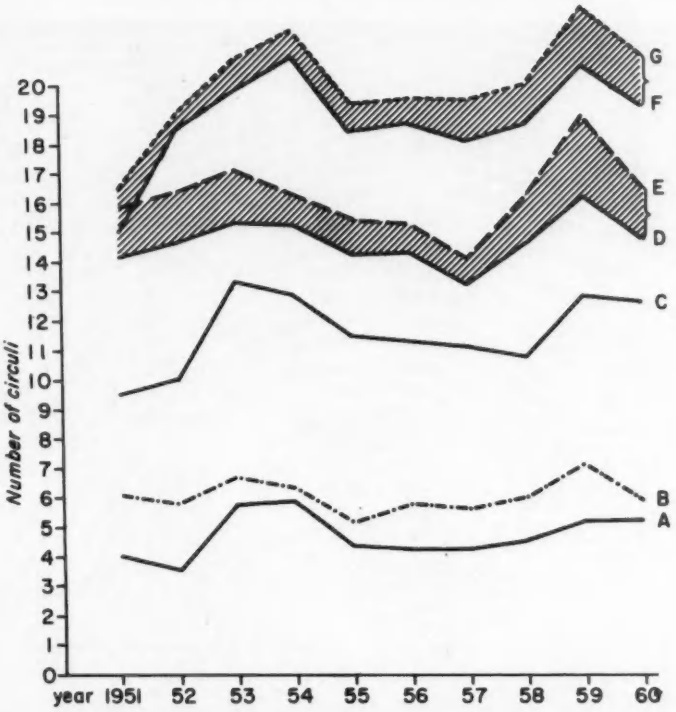

FIG. 1. Circuli counts in the lacustrine part of sockeye scales from Ozernaya River. Average number of circuli formed up to: A, first year in *3.* salmon; B, first year in *2.* salmon. C, second year in *3.* salmon; D, second year in *2.* salmon; F, third year in *3.* salmon. Average total number of freshwater circuli in: E, *2.* salmon; G, *3.* salmon. Shaded areas designate spring growth in year of migration: *Top* — *3.* salmon. *Bottom* — *2.* salmon.

show three circuli less than scales taken between the dorsal and adipose fins. Still, the difference is substantial, and it may be rewarding to study in detail the difference in freshwater growth pattern between Ozernaya and Bristol Bay salmon. Since only *2.* fish are common to these two systems, a strong possibility exists that a partial segregation can be made of these two components of the high seas commercial sockeye catches by examining the freshwater area of the scales.

Such a technique may even be improved by using annual mean values for the two stocks rather than overall means to compensate for the inter-year variation seen in Fig. 1.

In this study, scale parameters were determined with the aid of a FORTRAN program written by Larry E. Gales (FRG 288). The input consists of circulus counts and radial distances of the scale. The output will yield any scale character and its variance commonly used, combinations of different characters,

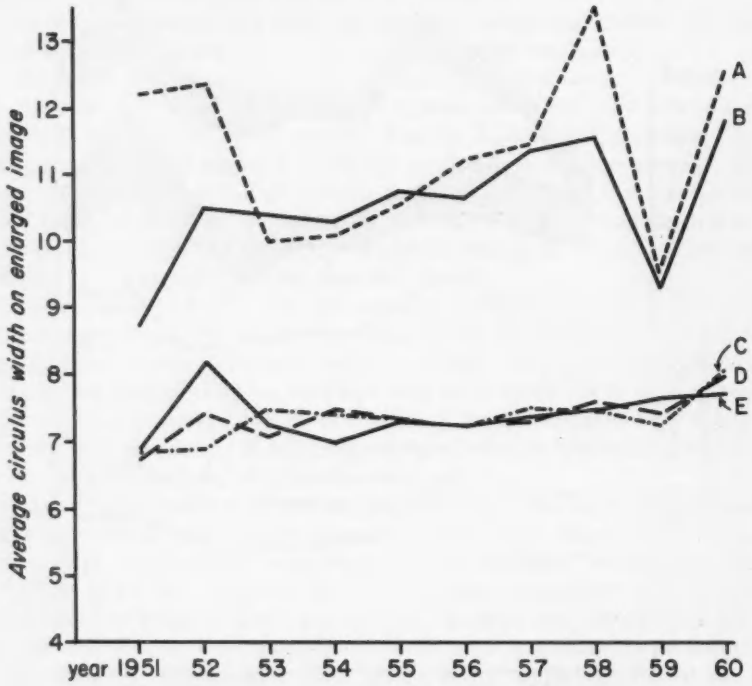

FIG. 2. Relative circuli width in the lacustrine part of sockeye scales from Ozernaya River. Average circuli width during: A, first year in *3.* salmon; B, first year in *2.* salmon; C, second year in *3.* salmon; D, third year in *3.* salmon; E, second year in *2.* salmon.

and plotted histograms, as well as card punch-out for use in further analysis, such as analysis of variance or discriminant analysis.

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(Fig. 3 *opposite*)

FIG. 3. Scale of sockeye salmon from Ozernaya River with three freshwater annuli.

An Occurrence of Capelin (*Mallotus villosus*) in the Bay of Fundy

So seldom do capelin, *Mallotus villosus* (Müller), occur in the Bay of Fundy that their appearance there in substantial numbers during the winter and spring of 1965 is worthy of record.

Sporadic occurrences of capelin in the Bay of Fundy since 1850 have been reported by Perley (1852), Kendall (1917, 1919), Huntsman (1922), and Bigelow and Schroeder (1953). The last official record of capelin in the Bay of Fundy was reported by Bigelow and Schroeder (1953), as having occurred in May 1915 and being frequently taken in the vicinity of Passamaquoddy Bay from then until March 1919.

Some authors, notably Bean (1880), Jordan and Evermann (1896), and Fowler (1911), give the Cape Cod region of Massachusetts as the southern limit of *Mallotus* in the western Atlantic. However, Goode and Bean (1879) wrote, "It has not been recorded south of Halifax." Atwood (1872) said, "It does not come as far south as New England"; and Goode (1884), "It never approaches the shores of New England." Hardy (1867) considered the southern limit of capelin to be Louisburg, Cape Breton, where "its visits are not always annual or certain." Jones (1879) said, "It occurs as far south as Halifax only occasionally."

It seems, therefore, that while there may be some question about the occurrence of *Mallotus* as far south as Cape Cod, there is no doubt whatsoever that it has occurred sporadically in the Bay of Fundy and in the Gulf of Maine prior to 1965.

Between March 23 and May 12, 1965, more than 80,000 lb of capelin were caught in the Bay of Fundy. The catches were made in Passamaquoddy Bay and along a short stretch of coast between Deadman's Harbour and Seeley's Cove (a straight line distance of about 10 nautical miles). All of the catches were made in herring weirs.

Enquiries were made at various localities in Yarmouth and Digby Counties on the Nova Scotia side of the Bay of Fundy, at Grand Manan, Deer Island and Campobello, New Brunswick, and along the coast of Maine as far as Boothbay Harbor. We could discover no evidence of capelin being caught or seen in any of these areas. However, some of these enquiries turned up interesting observations, especially in view of the fact that there is no written record of capelin occurrence in the Bay of Fundy between 1919 and 1965. Some fishermen in the area were not at all surprised to see capelin while their next-door neighbours had never even heard of them. Some said they occur every few years, while others said that, to their knowledge, capelin had never occurred in the Bay of Fundy before 1965. A fishery officer recalled capelin occurring occasionally in small quantities in the weirs around Grand Manan

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between 1929 and 1934. A Campobello weir-fisherman reported very large quantities of capelin in his weir at Welchpool about 12 or 15 years ago. He recalled seeing them many times, but usually in small numbers only. Another Campobello weir and purse-seine fisherman had never heard of capelin. Two fishermen seined 3000–4000 lb of capelin at Chamcook in Passamaquoddy Bay, on one occasion during the autumn of 1949. Yet another fisherman who had operated a weir in Deadman's Harbour for 27 years was not familiar with capelin and thought they were smelt (*Osmerus mordax*).

Samples of capelin for length and age studies were obtained from catches made at Deadman's Harbour on April 12 and at Seeley's Cove on April 20. Total lengths were recorded, and ages determined from both scales and otoliths. The distributions of length for males and females in both the Deadman's Harbour and Seeley's Cove samples are given in Fig. 1. The mean lengths of the sample from Deadman's Harbour was 14.6 cm for males and 13.5 cm for females. In the sample from Seeley's Cove, the mean length for males was

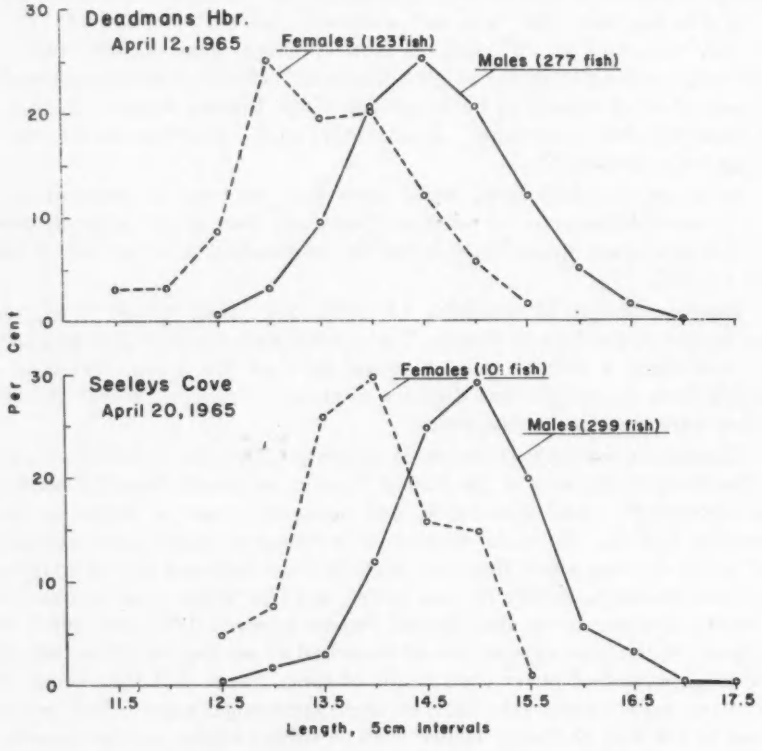

FIG. 1. Length-frequency diagrams for male and female capelin.

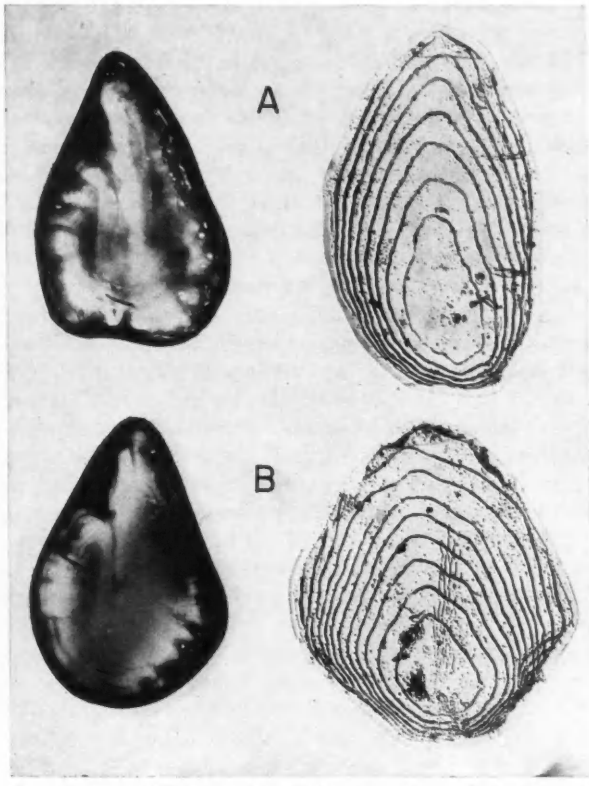

FIG. 2. Otolith and scale from (A) 1-year-old female capelin and (B) 2-year-old male capelin.

14.9 cm and for females 14.0 cm. The size range for both samples was from 12.5 to 17.3 cm for males and 12.3 to 15.6 cm for females.

The sizes of capelin reported by Templeman (1948) were considerably larger than those recorded here. Mean lengths of samples from Newfoundland varied from 16.41 to 19.00 cm for males with an overall mean of 17.76 cm for 59,042 fish. The size range was from 13.0 to 21.5 cm. For females, mean lengths varied from 13.33 to 17.47 cm with an overall mean of 16.08 cm for 23,567 fish. The size range was from 11.0 to 21.0 cm.

Age determinations were made on 35 male and 20 female capelin from Deadman's Harbour and Seeley's Cove. Twenty-eight males ranging in length from 14.0 to 16.5 cm were 2+ years of age (1962 year-class). The remaining seven were 1963 year-class fish (1+ years old) with a size range of 12.5–13.5 cm. Eighteen of the females were 1963 year-class fish (1+ years old) with a size range of 11.5–13.0 cm. The remaining two were 1962 year-class (2+ years old) with a size range of 13.5–16.0 cm. A scale and an otolith from a 1-year-old female capelin and from a 2-year-old male capelin are shown in Fig. 2.

Templeman (1948) noted that although the sex ratio in capelin is likely to be 1:1, there is a wide variation in samples taken during the spawning season. He found that at this time there is a partial division of the maturing female schools from the roving schools of males, and that the percentage of male capelin spawning on the beaches increases as spawning gets under way.

Capelin captured in Deadman's Harbour on April 12 were approximately 69% males, and those sampled in Seeley's Cove on April 20 approximately 75% males. It would appear, therefore, that these fish were partially segregated, as if on a spawning migration.

Spawning ridges were visible on male capelin captured in mid April at Deadman's Harbour, but they were by no means well pronounced. The ovaries of the females, however, appeared to be quite well developed with eggs having a mean diameter of 0.787 mm. When examined a month later at Seeley's Cove, ovaries contained eggs with a mean diameter of 0.818 mm. Templeman (1948) records a mean diameter of 0.965 mm and a range of 0.9006–1.0374 mm for extruded eggs in 10% formalin. Templeman judged that female capelin containing eggs from 0.59 to 0.92 mm diameter in mid May would mature in about a month. Male capelin showing only traces of spawning ridges could be found, up to a month prior to spawning. Capelin spawning does not occur on Newfoundland beaches until June.

Vertebral numbers were counted on a sample of 132 capelin. These were sexed and means calculated for both males and females. The mean number for 89 males was 66.03 and for 43 females it was 65.86. Because of the small number of fish in the samples, no statistical comparison between the means was made. It is interesting to note, however, that for both sexes the mean numbers are higher than those reported by Templeman (1948) for the Newfoundland area where means for males varied from 65.44 to 65.56 with an overall mean of 65.52 for 2789 fish, and means for females varied from 65.53 to 65.72 with an overall mean of 65.65 for 2770 fish. For all Newfoundland areas

sampled, the mean vertebral numbers for females were higher than that for males and the differences were statistically significant. In the Bay of Fundy the vertebral number for males was higher than that for females.

At present, no conclusions can be drawn concerning the sporadic occurrence of capelin in the Bay of Fundy. Sleggs (1933) stated that capelin are governed in their inshore movements by water temperature, avoiding water above approximately 10.5 C. Bigelow and Schroeder (1963) suggested that "the waves of capelin that occasionally invade the Bay of Fundy are carried thither by the ice-chilled Nova Scotian Current which brings water colder than 3 C along the Nova Scotia coast and into the eastern side of the Gulf of Maine at some time in the spring in most years."

Normal water temperatures for the first quarter of the year are 4.4 C in the Lurcher Lightship Vessel area and 3.1 C along the N.B. side of the Bay of Fundy. Records at the St. Andrews Station of the Fisheries Research Board of Canada show that during the first quarter of 1965 water temperatures were lower than normal by as much as 1.8 C at the Lurcher Lightship and 0.8 C along the N.B. side of the Bay (L.M. Lauzier, personal communication). It may be that the capelin's avoidance of warmer waters prevents its entrance into the Bay of Fundy except during an abnormally cold season.

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